THE UNIVERSITY OF ALBERTA

# HOW TEMPERATURE AND MORPHOLOGY INFLUENCE THE CALLING SONGS OF TWO SPECIES OF GRYLLUS

by

© ANGELINE ELAINE BURGESS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

SPRING, 1970

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "How temperature and morphology influence the calling songs of two species of Gryllus" submitted by A. E. Burgess in partial fulfilment of the requirements for the degree of Master of Science.

Abstract

The sound producing apparatus of male Gryllus veletis Alexander and Bigelow is very similar to that of male Gryllus pennsylvanicus (Burmeister). The calling songs of both species are composed of multi-pulsed chirps and sounded identical. Dominant frequency progressively decreased within each pulse because the file teeth are farther apart at the lateral end of the file. Pulse duration depended on the number of teeth struck per pulse, and was greater than pulse interval. Pulse rate followed a sigmoid pattern with an increase in temperature, with the slope 3.06 fold greater for G. veletis than for G. pennsylvanicus. For G. veletis, increased pulse rate was due to linear or concave decreases in pulse duration and pulse interval. With an increase in temperature there was a linear increase in dominant frequency which lagged behind the increase in pulse rate because pulse interval decreased faster than pulse duration. For G. pennsylvanicus, the relationship between temperature, pulse duration, pulse interval, and dominant frequency did not follow a discernible pattern.

Acknowledgements

I wish to thank Dr. G. Pritchard for supervising the early stages of this work, and Dr. D. Craig and Dr. B. Hocking for their encouragement and supervision of the latter stages. I am also grateful to Dr. B. Heming and Dr. A. Steiner (Department of Zoology) for their suggestions and criticism of this manuscript.

I am indebted to the Department of Zoology for the use of the sonagraph; to P. Reedyk in Lethbridge for his enthusiastic assistance in collecting crickets; to Dr. J. Barron for his advice on rearing crickets; to J. Scott of this Department and to Photographic Services, especially J. Dietrich, for their help with the photography; to Technical Services for their work on the sonagraph, and to my colleagues and friends whose help and support have been unflagging.

Autobiographical sketch

I completed grade twelve matriculation in North Battleford, Saskatchewan, received a B. A., honours biology, from the University of Saskatchewan, and a Professional Certificate in education from the University of Alberta. I taught senior high school in South Battleford, Saskatchewan for two years before entering graduate studies.

My interest in entomology began during my undergraduate years when I worked on mosquitoes for two summers as an assistant in a virology laboratory at the University of Saskatchewan. Dr. Hocking suggested a project on some aspect of sound production in insects, and I chose to work on crickets.

Table of contents page

1.0 INTRODUCTION AND HISTORICAL BACKGROUND. . . 9

2.0 EQUIPMENT AND METHODS. . . . . 27

2.1 Equipment . . . . . 27

2.2 Methods. . . . . 32

2.3 Sources of error. . . . . 35

3.0 OBSERVATIONS . . . . . 38

3.1 Tegminal morphology. . . . . 38

3.11 Areas of tegmina. . . . . 38

3.12 Venation. . . . . 42

3.13 Sound producing apparatus. . . . . 45

3.2 Calling songs . . . . . 55

3.21 Description of a chirp. . . . . 55

3.22 Effect of temperature change on pulse rate . . . . . 59

3.23 Effect of temperature change on pulse duration and pulse interval . . . . . 61

3.24 Effect of temperature change on dominant frequency. . . . . 63

3.25 Effect of temperature change on number of teeth struck per pulse. . . . . 65

4.0 DISCUSSION. . . . . 67

5.0 REFERENCES . . . . . 74

6.0 APPENDIX . . . . . 79

List of tables (APPENDIX) page

Table 1 Tegmina of G. veletis males: The percentage of the dorsal field occupied by each of its five subdivisions. . . 79

Table 2 Tegmina of G. pennsylvanicus males: The percentage of the dorsal field occupied by each of its five subdivisions. 80

Table 3 Tegmina of G. veletis and G. pennsylvanicus males: Areas of mirror, harp, and dorsal field. . . . . 81

Table 4 Tegmina of G. veletis and G. pennsylvanicus males: The relationship between number of file teeth, file length, and dorsal field area. . . . . 82

Table 5 G. veletis males: A comparison between the right and left tegmina. . . . . 83

Table 6 G. pennsylvanicus males: A comparison between the right and left tegmina. . . . . 84

Table 7 Tegmina of G. veletis males: The percentage of the total number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end. . 85

Table 8 Tegmina of G. pennsylvanicus males: The percentage of the total number of teeth found on each consecutive 10% of the length of the file from the medial to the lateral end. . . . . 86

Table 9 G. veletis and G. pennsylvanicus calling songs: Percentage of chirps with three, four, five, and six pulses. . . 87

Table 10 G. veletis and G. pennsylvanicus calling songs: Percentage of sonagram chirps beginning with faint, short, marks. . . . . 87

Table 11 G. veletis calling song: The relationship between temperature, pulse duration, and pulse interval. . . . . 88

Table 12 G. pennsylvanicus calling song: The relationship between temperature, pulse duration, and pulse interval. . . . . 89

Table 13 G. veletis calling song: The relationship between temperature and dominant frequency. . . . . 90

Table 14 G. pennsylvanicus calling song: The relationship between temperature and dominant frequency. . . . . 91

Table 15 G. veletis calling song: The relationship between temperature and grand average pulse rate. . . . . 92

Table 16 G. pennsylvanicus calling song: The relationship between temperature and grand average pulse rate. . . . . 93

Table 17 G. veletis calling song: The relationship between temperature and number of teeth struck per pulse. . . . . 94

List of figures page

Fig. 1 Sonagram of a four-pulsed chirp of a G. pennsylvanicus male. . . . . 28

Fig. 2 Sonagrams of the calling song of a G. pennsylvanicus male recorded at 25 C in four types of cages. . . . . 31

Fig. 3 Subdivisions of the dorsal field of the left tegmen of a G. pennsylvanicus male. . . . . 39

Fig. 4 Tegmina of G. veletis and G. pennsylvanicus males: The relationship between the areas of dorsal field and harp. . . . . 41

Fig. 5 Tegmina of G. veletis and G. pennsylvanicus males: The relationship between the areas of dorsal field and mirror. . . . . 41

Fig. 6 Venation of the left tegmen of a G. pennsylvanicus male. . 44

Fig. 7 Tegmina of G. veletis and G. pennsylvanicus males: The relationship between dorsal field area and file length. . 46

Fig. 8 Tegmina of G. veletis and G. pennsylvanicus males: The relationship between file length and number of file teeth. . . . . 47

Fig. 9 Left tegmen of a G. veletis male: The three groups of file teeth. . . . . 50

Fig. 10 Right tegmen of a G. pennsylvanicus male: The three groups of file teeth. . . . . 51

Fig. 11 Tegmina of G. veletis and G. pennsylvanicus males: The percentage of the total number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end. . . . . 52

Fig. 12 G. veletis and G. pennsylvanicus calling songs: The relationship between temperature and pulse rate. . . . . 60

Fig. 13 G. veletis and G. pennsylvanicus calling songs: The relationship between temperature, pulse duration, and pulse interval. . . . . 62

Fig. 14 G. veletis and G. pennsylvanicus calling songs: The relationship between temperature and dominant frequency. .64

Fig. 15 G. veletis calling song: The relationship between temperature and number of teeth struck per pulse. . . . . .66

# 1.0 INTRODUCTION AND HISTORICAL BACKGROUND

Man has known for thousands of years that insects make sounds, and for some hundreds of these years has been speculating as to how the sounds are made, and whether they serve any useful purpose. Scientific interest in insect sounds dates back at least to Aristotle, who, over 2000 years ago, separated two groups of Homoptera on the basis of whether or not they could produce sound (Myers, 1929).

Bioacoustic terminology has arisen empirically. Although the meanings of many of the terms are unambiguous, those of others vary depending on the region and discipline in which the terms are used and on the authors using them. The same word does not always have the same meaning, and what is worse, some of the meanings are completely different from those attached to the same word in physics. At a symposium on animal acoustics in Paris in 1954, the problem of standardizing terminology for Orthopteran sounds was discussed by French, German and English workers. No decisions were made, largely due to a lack of time.

Insect sounds are sometimes referred to as songs but strictly speaking these sounds are not songs because they have no melody (Alexander, 1960; Tuxen, 1967). Tuxen prefers to speak of insect voices. He does not object to the term song, especially in describing rhythmical, repetitious sounds reminiscent of the chants of primitive

man, as long as it is understood that this term is merely a poetic expression.

Haskell (1961) says the verb "to stridulate" comes from the Latin verb stridere, meaning to creak, and that the Oxford Dictionary definition, "make a shrill jarring sound by rubbing together of hard parts of body," is not accurate because some frictional mechanisms of sound production produce pleasant sounds, and some mechanisms other than frictional ones produce jarring sounds. He uses the term stridulation to describe any frictional mechanism of sound production even though he suggests that it should refer to any sound produced by an insect, and that a stridulatory mechanism should refer to any insect sound producing mechanism. I think the latter definition is too narrow in that it applies only to insects, and too broad to be of any value in describing insect sound production. Dumortier (1963) also uses stridulation to describe all sounds originating through the rubbing together of two surfaces even though etymologically the term stridulation may be applied to every emission of grating or piercing sounds.

The name pulse was first given to a biological event, the heart beat, dating back at least to Pliny, 23-79 A.D. (Myers, 1929). Its use in physics, which has not been traced back beyond the eighteenth century, was extended to include the wave form representing the heart

beat on paper or on the cathode ray tube, then to other wave forms of like character, and finally to a simple train of sine waves (ibid.). Evidence of its confused usage can be seen in "The Songs of Insects" by G. W. Pierce (1948), a physicist and amateur entomologist. On p. 71 he uses it in the sense of a wave (a cycle), on p. 26 to describe a wave-train, and almost everywhere else as equivalent to assemblages of wave trains. Pulse has, in part, the same meaning as that used by physicists, that is, for impulse modulation of the carrier frequency, but it is also used by most English and American authors for the sound emission produced by an entire movement of the stridulatory apparatus (Dumortier, 1963). These are the same in crickets, but in other insects such as field and leaf grasshoppers, one cycle of movement of the stridulatory apparatus would produce a biological pulse consisting of many physical pulses.

A chirp was defined by Broughton (1952) and Chavasse et al. (1955) for grasshoppers as the sound corresponding to a single movement of the stridulatory apparatus. Most English and American authors use the term for a regular group of pulses separated before and after by a silence (Dumortier, 1963). Pierce (1948), Alexander (1957a), and Walker (1957) spoke of unipulse and multipulse chirps, thereby giving a chirp a multiple concept.

Broughton (1963) says that in 1960 he circulated a draft review of suggested definitions to 36 bioacousticians throughout the world,

asking for their opinions. Except for the definition of pulse, he received overwhelming support from 12 of the 17 correspondents who replied. I will use the terms pulse and chirp in the sense that Broughton suggests. A pulse is a homogeneous parcel of sound waves of finite duration; a simple wave-train (i. e. one divisible into waves, but not into groupings of waves). Pulse duration refers to the time that elapses between the leading edge and the trailing edge of one pulse, and pulse interval refers to the time that elapses between the trailing edge of one pulse and the leading edge of the adjacent pulse within the same chirp. Pulse rate, in pulses per second, refers to the number of pulses of average duration, separated by pulse intervals also of average duration, which would be produced in one second if they were produced without other interruption.

A chirp is the shortest unitary rhythm-element of a sound emission that can readily be distinguished as such by the unaided human ear. A very long chirp with the constituent pulses resolvable by the human ear is called a trill. Chirp rate, in chirps per minute, refers to the number of chirps an insect would produce in one minute if it chirped without interruption at a fairly uniform rate.

Haskell (1961) outlined the following methods of insect sound production.

I. Sounds produced as by-products of some usual activity of the insect, such as walking, feeding, cleaning reactions or the beating

of the wings in flight.

II. Sounds produced by impact of part of the body against the substrate (some adult Coleoptera, Hymenoptera, Isoptera, Orthoptera, Plecoptera, and Psocoptera). Various parts of the body can be used for tapping, for example, the head (soldier termites, the Death Watch Beetle Xestobium), the tarsi (some Oedipodinae and tettigoniids), or the tip of the abdomen (a few Plecoptera, Tenebrionidae, and Psocoptera). Some Hymenopterous and Lepidopterous larvae produce sound by rubbing their anal segments against the leaf surface.

III. Sounds produced by special mechanisms. The number and variety of insects which produce sounds in this way exceed those of all other living organisms combined, but only a few of them make sounds loud enough to be noticeable to man (Alexander, 1957a). Three types of mechanisms exist:

A. A vibrating membrane apparatus is widespread in adult Cicadidae and Cicadellidae (Homoptera). It consists of paired tymbal organs on the dorso-lateral surface of the first abdominal segment. Each organ has a membrane, the tymbal, which is normally bowed outward, and a tymbal muscle attached to the center of the tymbal. Contraction of this muscle pulls the tymbal inwards producing a "click." When the muscle relaxes, the tymbal springs back to its original position due to its own elasticity, producing a second "click." To the human ear, the sound appears continuous.

Hinton (1948) applied the name tymbal organ to a sound producing apparatus on the thorax of some Arctiidae and Syntomidae (Lepidoptera). The tymbal, a modification of the metepisternal sclerite, forms a membranous covering over a cavity. Rapid contraction of the dorso-ventral flight muscles alters the shape of the cavity, causing the tymbal to vibrate with a crackling sound.

B. Special mechanisms directly involving air movement are found in adult Orthoptera, Lepidoptera, Coleoptera, and Hymenoptera.

The epipharynx of the deaths head hawk moth, Acherontia atropos Linnaeus, interrupts the movement of air which the pharynx and its associated muscles suck up the proboscis. The resulting pulsed air stream produces loud squeaks.

Many insects can emit poisonous froth or unpleasant liquids from certain spiracles, and such emissions may be accompanied by audible noises (Haskell, 1961). The bombardier beetles Brachinus can spray fluid from abdominal glands accompanied by an audible sound.

According to Woods (1959), the piping of a queen honey bee is probably produced by a modulated air stream passing into or out of the spiracles. The frequency of the wing vibration is thought to be detected by proprioceptors which, by way of the central nervous system, determine the rate of opening and closing of the spiracles. Spiracular mechanisms have been suspected in various Diptera, but no modern work has been done with them (Haskell, 1961).

C. The greatest number and variety of insect sounds are produced by stridulation. Many adult Orthoptera, Coleoptera, Heteroptera, Lepidoptera, and a fewer species of adult Homoptera, Diptera, and Hymenoptera stridulate. Alleged stridulatory apparatus have been described in Psocoptera and Thysanoptera on purely morphological grounds, but their sound producing function is hypothetical (ibid.). Among immature insects, stridulation occurs in certain larvae and pupae in Coleoptera and Lepidoptera, pupae in Hymenoptera, and nymphs in Heteroptera, Odonata, and Orthoptera.

In general, stridulatory apparatus are of similar construction and consist of a surface bearing a series of ridges or projections called the file, and a hard ridge or knob called the scraper. During stridulation the scraper is drawn across the file. The file and scraper may be on the head or head appendages, thorax, abdomen, tegmina, wings or legs, or involve a combination of any two of these body parts. In Orthoptera, the principal sound producing Order, tegminal stridulation and tegmino-femoral stridulation are the most widespread.

Crickets (Orthoptera: Gryllidae) are the most renowned musicians amongst insects. Each tegmen bears a complete song producing apparatus which can be divided into two groups: The primary song producing structures, the file on the ventral surface and the scraper on the dorsal inner margin, and the auxiliary structures, membranous parts of the tegmen which are also set into vibration. During stridulation

the tegmina are raised and moved laterally across one another, usually with the right tegmen uppermost (Lutz, 1908; Lutz and Hicks, 1930; Rakshpal, 1960; Huber, 1962; Bigelow, 1964), so that the functional file is usually on the right tegmen and the functional scraper on the left tegmen.

Alexander (1963) studied the songs and associated behaviour of 89 species of crickets representing 20 genera and eight subfamilies. He described six functional kinds of songs which operated only amongst adults of the same species, and only in connection with activities related to reproduction. These were the calling song, courtship song, courtship interruption song, post-copulatory song, aggressive song, and recognition song. Most species had a repertoire of at least four songs. If the repertoire consisted of just one song, that song was always the calling song. This thesis will deal exclusively with the calling song.

The calling song is the one most commonly heard because it is the loudest, most rhythmical,and most persistant of all the songs. It is produced by mature males who have not copulated recently. The presence of a spermatophore in the spermatophore pouch is necessary for the production of the calling song in Gryllus campestris (Linnaeus) but not in Miogryllus (Gryllinae) or Anurogryllus (Brachytrupinae) (Alexander, 1962, 1966). Gryllus veletis Alexander and Bigelow and Gryllus assimilis

Fabricius begin singing before their first spermatophores are developed, and removing developed spermatophores artificially does not inhibit the calling song (Rakshpal, 1960). Certain environmental factors also determine whether or not the calling song is produced. Most crickets sing only under humid conditions, many sing mainly in the dark or at very low light intensities, some seldom sing except during the day, and others sing regularly both day and night. Mechanical disturbances, heavy wind and rain, and very high or low temperatures inhibit singing. Silent males are stimulated to sing in response to the calling songs of other individuals. When temporary contact with other crickets results in the production of temporary aggressive or courtship songs, it usually ultimately results in an adjustment to the calling rhythm and long-continued production of the calling song. This could occur either through external auditory feedback, some kind of internal feedback or both (Alexander, 1961).

Upon hearing the calling song, sexually responsive females move in a fairly straight line towards the male (Alexander, 1960). This is at variance with the findings of Haskell (1953) with Gryllus domesticus Linnaeus, where the calling song caused continuous short bursts of locomotor activity. The calling song has a greater variety of effects on other males of the same species than on the females. By repelling subordinate males, the calling song is important in the spacing of territorial crickets, who remain only within hearing range of each other (Alexander, 1961). It has already been

mentioned that the calling song can stimulate a silent male to start singing. Even in species that do not synchronize their chirps (chirp with the same chirp rate and continuously in phase), individuals in a field do not sing independently of each other, but alter their rate or rhythm so that they sing in bursts separated by intervals where none or only a few crickets are singing (Alexander, 1957a). At close range, the calling song evokes aggressive song and aggressive actions such as antennal whipping, kicking with the hind or fore-legs, and biting with the mandibles.

Pioneers in bioacoustics were handicapped by the lack of electronic instruments with which to record and analyze sounds. They could only describe them onomatopoetically and by aurally comparing them with known frequency sources such as tuning forks or musical scales. Only an accurate watch is needed to determine chirp rate however, and early experiments dealt with this parameter of the calling song. Brooks (1881) was the first to report in the scientific annals that there was a remarkable accordance between chirp rate (species not given) and air temperature. Dolbear (1897) expressed the relationship between chirp rate and air temperature by a straight line with the equation $^{o}F = 50 + \frac{N - 40}{4}$ (N = chirp rate), which later became known as Dolbear's Law. He did not give the species, but from his description of the song and behaviour, Bessey and Bessey (1898) thought it was probably Oecanthus niveus (DeGeer), the snowy tree

cricket, often referred to as the temperature cricket. They found that the relationship between chirp rate and air temperature was expressed by a curve. Between 60 F and 80 F the air temperature predicted by a straight line having the equation $^{o}F = 60 + \frac{N-92}{4.7}$ was one to two degrees lower than the actual air temperature. Below 60 F and above 80 F, the predicted air temperature was two to three degrees higher than the actual air temperature. They concluded that Dolbear had oversimplified the relationship, and that the designation "Law" for his equation was not justified. Edes (1899), Schull (1907), Fulton (1925), Allard (1929, 1930 a, b), Lutz (1938), Pierce (1948), Hallenbeck (1949), and Frings and Frings (1957) had no doubt that air temperature influenced the chirp rate of Oecanthus, Nemobius and Gryllus species, but the exact relationship had not been demonstrated beyond question. They suggested that a number of other environmental factors such as humidity and wind velocity as well as genetic, behaviouraland physiological factors also influenced the chirp rate.

Dolbear (1897) sparked a heated controversy by claiming that individuals of O. niveus in the same field chirped synchronously. Edes (1899) and Schull (1907) regarded this phenomenon as an illusion, and thought Dolbear probably mistook the continuous chirping of one cricket for a chorus. Allard (1917) agreed that synchronous chirping occurred, but thought Dolbear had exaggerated when he stated all crickets in one field chirped synchronously. There were always a few in the

group who chirped asynchronously. Fulton (1934) showed experimentally that synchrony existed, by removing the auditory organs of males that chirped synchronously and noting that they were no longer able to do so. Only night-singing crickets that live in trees or tall shrubs sing synchronously (Alexander, 1960).

With the advent of electronic instruments, there was an upsurge of interest in bioacoustics. Lutz and Hicks (1930) recorded and reproduced the sound of G. assimilis with a movietone camera. For the first time it was seen that a chirp is made up of a number of pulses which sound continuous, or at best slightly wobbly to the human ear. Lutz and Hicks did not solve the problem of whether a pulse was produced during tegminal upstroke, downstroke, or both. They believed, however, that a pulse was probably produced during every upstroke and every downstroke so that the pauses between pulses within a chirp (about 0.017 sec duration) would represent the time required by the cricket to change the direction of tegminal movement. They thought these pauses were too short to represent the time needed for the tegmina to get back to the starting point, which would be the case if a pulse was produced during either the downstroke or the upstroke.

Pierce (1948), using motion pictures of tegminal movement and simultaneous sound records, showed that G. assimilis produced sound only during the closing stroke of the tegminal motion cycle. Alexander (1966)

said that all crickets he recorded appear to sonify only during the closing stroke.

Cricket calling songs have a single strongly dominant frequency of from two to 10 kilocycles per second, which accounts for their unique musical quality (Alexander, 1962). In general, smaller crickets have the highest pitched songs (ibid.). Lutz and Hicks (1930) noticed that no pulse had more cycles of sound waves than there were teeth on the file. Each pulse started and ended faintly; the teeth at each end of the file were the least distinct and could possibly account for this. They suggested that each tooth strike caused one cycle of sound, and that the dominant frequency was determined by the number of file teeth scraped per second which in turn would depend on the spacing of the teeth and the speed of tegminal motion (i.e. a dominant frequency of five kcps would mean that 5000 teeth were struck per second).

Pierce (1948) verified this. He found that the number of sound waves emitted in one pulse of G. assimilis (calculated by multiplying the duration of the pulse by the dominant frequency) would be equal to the number of teeth struck during this pulse if 47% of the teeth on the file were used. The ratio of the downstroke in millimeters, obtained from the motion pictures, and the total length of the file in millimeters was indeed 0.47. According to Walker (1962), who worked mainly with a sonagraph, there is no completely satisfactory technique for

determining the duration of a pulse or the number of teeth struck during a pulse.

The mechanism that allows tooth-strike rate to determine the dominant frequency operates as follows: as the scraper strikes each tooth, a thrust is given in one direction to the file and in the opposite direction to the scraper. These thrusts are transmitted to the respective tegmina at the same frequency. The fundamental frequency is accompanied by a series of harmonic frequencies having two, three, four ... times the fundamental frequency (Pierce, 1948). The tegmina vibrate up and down once (they are quickly damped by air resistance because they are soft and only a small basal part attaches them to the thorax) producing one rarifaction and one condensation of the surrounding air. There can be additional frequencies due to the resonance of the tegmen as a whole or in parts,and harmonics may exist for each of these resonant frequencies. The dominant frequency is independent of the resonant frequency however. The resulting sound will be louder at the driven frequency, caused by the scraper striking the teeth. In gryllids, the tooth-impact frequency is equal to, or nearly equal to, the resonant frequency (the tegmina seem to vibrate as a whole) which helps explain the continuous emission of a fairly pure note (Haskell, 1961).

Since the calling song functions to bring males and females of the same species together, the question that arises is to which

parameter or parameters of this song the female reponds to. Regen (1913) saw that an unmated G. campestris female was attracted to the calling song of a male of the same species even when the sound came over the telephone, badly distorting the frequency. Pumphrey and Rawdon-Smith (1939) showed that a tympanic organ-auditory nerve preparation of a locust was insensitive to low frequency tones (50 - 3000 cps). It gave completely random responses to pure high frequency tones. A high frequency tone modulated at any frequency up to three kcps elicited bursts of activity at the modulation frequency. The pattern of impulses along the auditory nerve was unaffected by large changes in the carrier frequency. They concluded that information on the pulse rate and pulse rhythm patterns, not information on the frequency, was transmitted to the central nervous system. In the light of this knowledge, Regen's observations, mentioned above, are explained by the fact that the telephone did not affect the modulation frequency of the calling song, and enough carrier frequency was getting through to excite the female's tympanum. In summary, the dominant frequency of cricket calling songs merely acts as a carrier frequency. Because the sound is produced only during tegminal closing, this carrier frequency is amplitude modulated to produce pulses. Although the carrier frequency, in itself, plays no role in the responsiveness of the females, it must be within their hearing range in order to transmit the information (pulse rate and pulse rhythm pattern) carried by the pulses. Gross

differences in the dominant frequency occur at the level of genus or subfamily, and rarely among species in the same genus (Alexander, 1962).

In species whose calling song has a trilling rhythm pattern, the female responds to the pulse rate (Walker, 1957; Alexander, 1962). Alexander classified the chirping rhythm pattern into three categories, each one varying in the parameter to which the females of the same species responded. These categories were:

1. Chirps of intermediate length (3-7 pulses) delivered at an intermediate rate (100-300/minute) and somewhat irregularly. Females of these species responded to the pulse rate.

2. Long chirps (6-15 pulses) delivered slowly (50-200/min ) and regularly. Females of these species seemed to respond to the chirp rate and chirp length. This fits in with Walker's finding (1957) that females of Oecanthus species, whose males produced regular chirps, responded to artificial pulseless chirps.

3. Short chirps (2-3 pulses) delivered rapidly (300-900/min ) and regularly. Again, females of these species seemed to respond to the chirp rate and chirp length. Alexander suggested that perhaps they also responded to the continuity or discontinuity in chirp sequences.

In each of the above categories, the parameter to which the females responded was also the one which varied the least within the calling songs of individuals of the same species. In categories two

and three, Alexander thought that perhaps the pulse rate strengthened the response to the chirp rate. Walker (1962) said that with the exception of Nemobius carolinus Scudder, the calling song of every species he has worked with had a single characteristic pulse rate at a given body temperature. The calling song of N. carolinus is a trill with smooth (no audible periodic changes in intensity) portions alternating with pulsating portions. The pulse rate during smooth portions was less than during the pulsating portions.

Closely related species which breed at the same time and place have distinctive calling songs which prevent disadvantageous gene exchange; for these species, the calling song is now regarded as one of the best taxonomic characters (Bigelow, 1964). Sympatric species whose breeding seasons are seasonally isolated, or geographically isolated species, may not only have identical calling songs, but nearly identical repertoires (Alexander, 1962).

Armed with electronic equipment and a greater knowledge of the physical aspects of the calling song, investigators again focused attention on the effects of the environment on the nature of the calling song.

According to Walker (1962), humidity, sound, and temperature are the only features of the external environment known to affect the nature of the calling song. He found that lower relative humidities sometimes resulted in lower pulse rates, probably because of reduced

body temperature due to increased evaporation. However, the reduction was slight and so highly variable, even with the same individual under the same external conditions, that he dismissed the effects of humidity as being too small to be of any significance under field conditions. Sound influenced the chirp phase of crickets that synchronized their chirps and, as mentioned before, sometimes altered the chirp rate of species which did not synchronize their chirps. This was accomplished by changes in the chirp interval and the number of pulses per chirp. Pulse rate remained the same. Walker did not notice any effect of age, fatigue or conditioning on the nature of the calling song. Damage to the tegmina resulted only in a decrease in the intensity and a greater range of frequencies.

Most cases of variation in the calling song of geographically separated populations of a single species and of individuals within a local species population are slight, and are probably due to genetic differences (Fulton, 1933; Alexander, 1957b; Alexander and Thomas, 1959; Bigelow, 1960; Walker, 1962).

Our knowledge of insect songs is still in its infancy, and many interesting discoveries can be anticipated.

I will attempt to correlate morphology with function of the tegmina of Gryllus veletis and Gryllus pennsylvanicus, and to study the effect of temperature on their calling songs.

# 2.0 EQUIPMENT AND METHODS

## 2.1 Equipment

A Uher 4000 Report-L tape recorder with a frequency response from 40 to 20,000 cps at $7\frac{1}{2}$ inches per second, and a Uher M 514 microphone with a frequency response from 70 to 14,000 cps, were used. The magnetic recording tapes were Ampex 1.5 mil polyester.

The sonagraph was manufactured by the Kay Electric Company, Pine Brook, New Jersey. The input signals go through a record-reproduce amplifier and are recorded continuously on a magnetic disc that is driven at 24 revolutions per second by a synchronous motor. The recorded signals are erased after one revolution of the drum by an erase head, so that approximately the last 2.442 sec of the input signal remain on the magnetic disc. This recording is reproduced repeatedly at 3.33 times the original recording speed. A piece of dry facsimilie paper is wound around the drum which rotates synchronously with the magnetic disc. As the drum rotates, the stylus moves upwards and a slightly different portion on the signal spectrum is scanned by either a 45 cycle or a 300 cycle band-pass filter. Where the frequencies scanned for occur, a current is sent up to the stylus and a mark is made on the paper. The end result is a sonagram (fig. 1) which, according to the manual, should portray the frequency region from 85 to 8,000 cps. In practice it was found to portray only from 85 to 7,000

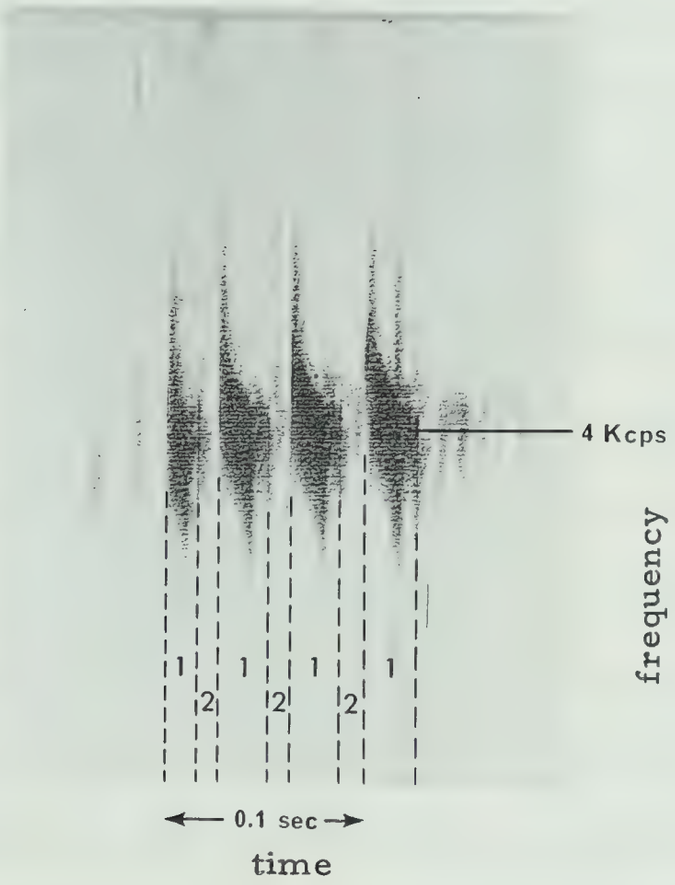



Fig. 1. Sonagram of a four-pulsed chirp of a G. pennsylvanicus male. X 1.7 (1 = pulse; 2 = pulse interval)

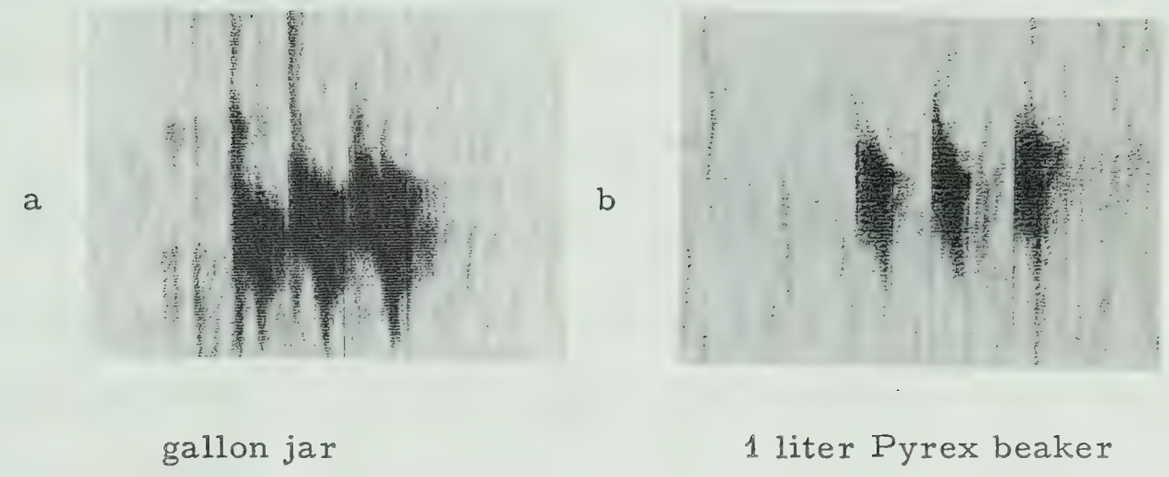
cps in a vertical distance of 9.55 cm. One revolution of the drum, which takes approximately 2.442 sec, covers a horizontal distance of 31.75 cm on the sonagram. The darkness of the mark gives an indication of the relative intensity of various parts of the recorded signal. The range in intensity that can be satisfactorily portrayed in any sonagraph is about 20 decibels. To get definite db figures on actual loudness would require the use of a sound level meter under standard conditions with the animal itself.

Cages used for recording animal sounds should be constructed from material that will not reverberate or reflect sound waves. Frings (personal communication), in his earlier work with insect sounds, found that in some glass containers, the reverberation and development of standing waves affected the sound patterns obtained, especially the pulse duration; in other glass containers, however, the pulse duration was apparently not affected. He now uses cages made of wood, not too tightly put together, with plastic screening.

I put G. veletis and Gryllus pennsylvanicus (Burmeister) into polystyrene foam and styrofoam cages, but they never sang. In the latter cage, perhaps they were agitated by methyl chlorine gas which may have been emitted when their tarsi pierced the styrofoam. Figure 2 a-d shows sonagrams of the calling song of a specimen of G. pennsylvanicus recorded at 25 C in a gallon jar with a narrow mouth, a one liter Pyrex beaker, a cage made from wire screening stapled together, and a cage

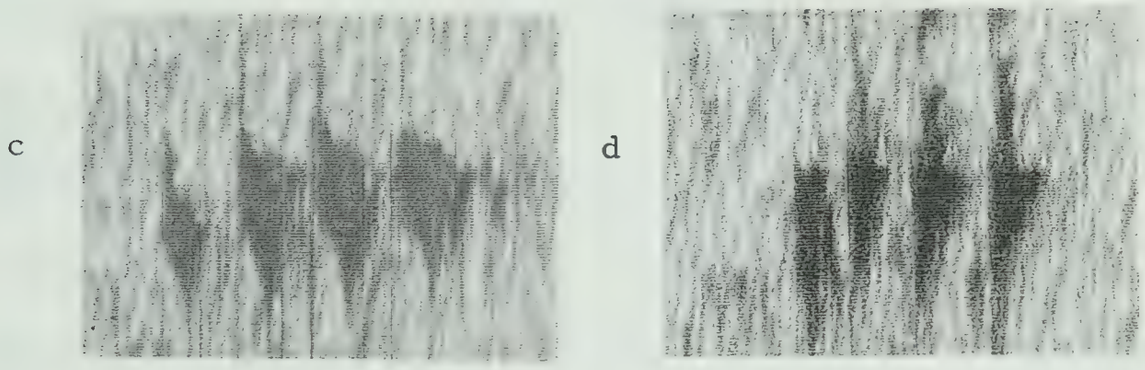
made from plastic (lucite) screening supported on a wooden frame. Recordings were easier to make using glass cages because the crickets could not climb up the sides and the microphone could be held stationary. It can be seen that the type of cage used greatly altered the shape of the pulses, especially the pulse duration. The sonagram from the recording in the beaker appears to have the sharpest pulse edges.

Unfortunately, recordings of all the G. pennsylvanicus and most of the G. veletis calling songs were made in gallon jars before the above experiment was conducted; sonagrams from most of these recordings, depending on the amount of background noise, were too poor to be of much use. The remaining G. veletis calling songs were recorded in the 1 L beakers. The data which will be given for G. veletis were obtained only from sonagrams made from the recordings in the beakers; the data for G. pennsylvanicus were obtained by choosing the clearest sonagrams from the recordings in the gallon jars.



a gallon jar

b 1 liter Pyrex beaker



c wire cage

d lucite cage

Fig. 2. Sonagrams of the calling song of a specimen of G. pennsylvanicus recorded at 25 C in four kinds of cages. X 1.5. Ordinate = frequency, abscissa = time.

2.2 Methods

Males of G. veletis and G. pennsylvanicus from Lethbridge, Alberta, and their laboratory-reared first generation offspring were used in these tests. Each was given a key number, and placed individually in a cage with rabbit pellets and a test tube of water plugged with cotton.

The crickets were held in the test room for at least half an hour before recordings were made so that their body temperature was in equilibrium with that of the environment. During this period the air temperature in the cage was taken every five minutes with a thermometer calibrated to fifths of a degree. Recordings were made at whatever temperature existed at the time. The test tube of water was removed, the microphone was suspended in the cage approximately six inches from the cricket, and the calling song was recorded at a tape speed of $7\frac{1}{2}$ ips. The air temperature where the cricket had been singing was taken again immediately after the recording and the average temperature calculated. The relative humidity determined at each experimental temperature always remained between 30% and 40%. The crickets were moved into rooms with different temperatures, and the above procedure was repeated.

Tape recordings of the calling songs of nine specimens of G. veletis at 22 different temperatures ranging from 15.2 C to 32.8 C, and 10 specimens of G. pennsylvanicus at 12 different temperatures ranging from 22.6 C to 28.6 C, were analyzed. This was done by

connecting the tape recorder by co-axial cable to the sonagraph. Each recorded sound was fed into the sonagraph at tape speeds of $3\frac{3}{4}$ and 1 7/8 ips as well as at the $7\frac{1}{2}$ ips at which it was recorded, in order to pick up any frequency components above eight kcps, and in order to spread out the time elements to facilitate their measurement. Only the wide band-pass filter of the sonagraph was used, giving the best resolution of the time elements on the sonagrams.

Sonagram measurements of pulse duration, pulse interval, pulse rate, and dominant frequency were made on the same three consecutive chirps from each cricket at a given temperature. Pulse duration was obtained by measuring the width of the pulse on the sonagram, and pulse interval was obtained by measuring the distance between the trailing edge of one pulse and the leading edge of the adjacent pulse within the same chirp. Since the pulses were interrupted within one second to form chirps, pulse rate was calculated from the data obtained from a chirp on the sonagram:

$$\text{pulse rate} = \frac{n}{d} \times v$$

where: d = the distance in cm between the leading edges of the first and last pulse in this chirp

n = the number of pulses in the chirp between d

v = the drum speed in cm/sec (13 cm/sec)

Dominant frequency of a pulse was obtained by taking the mean of the highest and lowest dominant frequencies which were read off a frequency

template made by using the sonagraph's built-in calibrator.

Each pulse within a chirp was given a number, with number one referring to the first pulse within the chirp. The grand average duration of each of the numbered pulses was obtained by taking the average duration of pulses with the same number for three chirps analyzed at $3\frac{3}{4}$ ips, then taking the average duration of the same pulses analyzed at 1 7/8 ips, and finally calculating the grand average duration of each of the numbered pulses. The same procedure was followed in calculating the grand average duration of each pulse interval, the grand average pulse rate, and the grand average dominant frequency of each of the numbered pulses, except that for the last two measurements, the three consecutive chirps were analyzed at $7\frac{1}{2}$ ips as well as at $3\frac{3}{4}$ ips and 1 7/8 ips.

2.3 Sources of error

The air temperature in the cage did not fluctuate more than ± 1 C during the half hour before a recording was made, but the cricket's body temperature may not have been the same as the average air temperature recorded. Variation in humidity may have altered the pulse rate slightly.

The rooms in which recordings were made were not soundproof; sonagrams of chirps recorded in rooms with background noise have a blur of black marks which mask the outline of the pulses, making measurements difficult. Frings (personal communication) suggests that reflections and reverberation of the walls of the room as well as those of the cage, could cause some frequency distortion of the sound being recorded, and may also account for the fact that the trailing edge of a pulse is seldom sharp. The effect on pulse duration of the kind of material used to construct the cage has already been discussed.

All recording equipment distorts sound. Harmonic distortion, given in percentage of the fundamental frequency, is the most common type of distortion; harmonics of two and three times the fundamental are introduced. I was unable to obtain the percentage by which the Uher 4000 Report-L distorts recorded sounds. The best tape recorders claim a small fraction of 1% distortion; a 2% to 4% distortion is acceptable for music and speech. This recorder has a flat response which varies within ± 3 db between 60 and 14,000 cps (manual), however

this variation would contribute very little to harmonic distortion.

Most recording equipment is designed for speech and music, where the higher frequencies have the lower intensities, consequently, the preamplifier of the recorder is designed to pre-emphasize them during playback. The energy distribution of most biological sounds, including cricket sounds, is not known, and there is the danger that pre-emphasis will be applied to frequencies which already have a high intensity. This could increase the distortion of some frequencies by overloading the tape, the amplifier or both. It would also limit the amplitude of lower frequencies. The noise produced by the Uher 4000 Report-L is 56 db below the loudest recording level, and normally would not contribute appreciably to background noise, but trying to increase the amplitude by turning up playback gain gives a higher noise level.

Tape movement is not uniform in any tape recorder. In theUher 4000 Report-L, wow and flutter combined vary ± 0. 15% at $7\frac{1}{2}$ ips (manual). This could affect sonagram measurements of pulse rate, pulse duration, and pulse interval, although not to any great extent.

The M 514 microphone has a flat response which varies within ± 3 db over its frequency response range, but again, this would contribute very little to harmonic distortion and background noise. The cardioid pattern of this microphone must be kept in mind when directing it towards a sound source. There will be an intensity difference

of 20 db between sound entering the microphone straight on, and the same sound entering the microphone at a 90 degree angle.

Many factors can thus affect the intensity of sounds reproduced on tape. The difference in the shape of some of the sonagram pulses, and the absence of faint, short marks at the beginning of some chirps could be due to certain frequencies having such a low intensity that they do not show up on the sonagrams.

Frings (personal communication) who has studied sound production in both insects and marine animals, considers the sonagraph a poor instrument for any sort of sound analysis. Where sounds are pulsed, as cricket sounds are, the pulse rate can be modulated upon the frequencies of the sound to produce more complex patterns. These secondary patterns would interfere with sound analysis, and might be the cause of the problems encountered when recording under reverberant conditions. He says that a sonagram without an accompanying oscillograph may be next to useless, and that this view has recently been supported by studies at the Marine Biological Laboratory in Woods Hole, Massachusetts.

Pulse duration, and therefore pulse interval, depends partly on where the marking intensity of the sonagraph is set. Both were difficult to measure because the transition from sound to silence is seldom sharp. The sonagraph's time scale accuracy limit is 1.5 msec.

The upper and lower frequency limits of a pulse are not sharply demarcated. The sonagraph's accuracy limit for frequency is 45 cps.

# 3.0 OBSERVATIONS

## 3.1 Tegminal morphology

### 3.11 Areas of tegmina

The tegmina of G. veletis and G. pennsylvanicus are tough and leathery, and when closed, they form a box-like cover for the proximal part of the abdomen. The right tegmen was uppermost in all of the crickets I studied. Each tegmen is folded longitudinally along the stem of the medial vein to form a dorsal and a lateral field. A series of fan-like folds along the branches of the media forms the median fan, which allows for the tapering of the abdomen. The dorsal field is divided into five subdivisions: the basal area, the harp, the cordal area, the mirror,and the apical area (fig. 3).

The tegmina from ten randomly-selected specimens of G. veletis and ten randomly-selected specimens of G. pennsylvanicus were mounted on slides, photographed, and the prints enlarged to give a magnification of 18.4 times. The area of each of the five subdivisions of the dorsal field was measured with a planimeter. Tables 1 and 2 show the percentage of the dorsal field occupied by each of these subdivisions for G. veletis and G. pennsylvanicus respectively. For both species, the five subdivisions, in order of increasing area, are: mirror, apical area, cordal area, basal area,and harp.

Figures 4 and 5, plotted from the data in table 3, show that for both species the areas of the mirror and harp increased linearly with

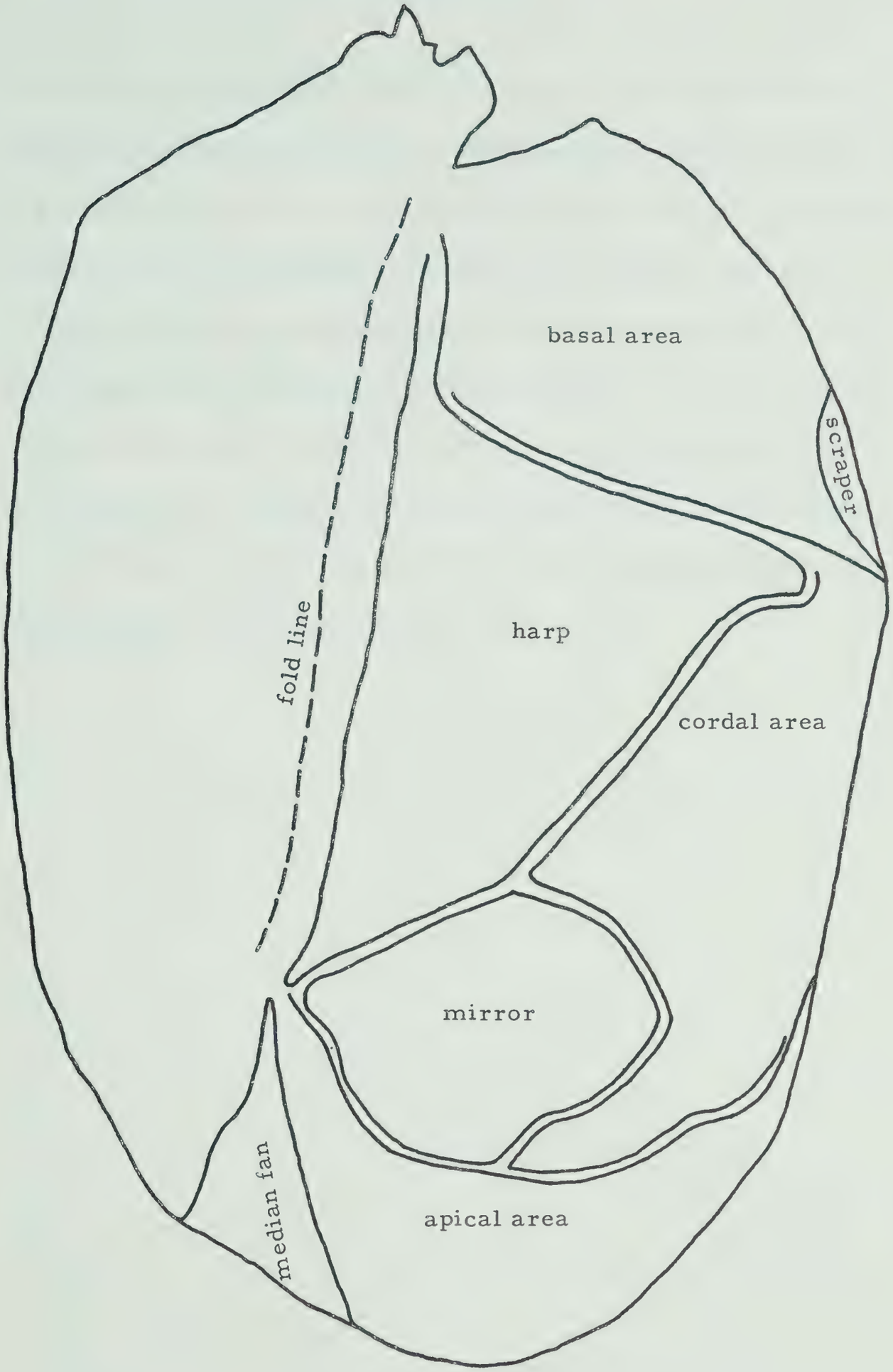



Fig. 3. Subdivisions of the dorsal field of the left tegmen of a G. pennsylvanicus male. X 20

an increase in dorsal field area. In all cases, the correlation coefficients for the regression lines show that there is less than one chance in a hundred that these relationships were due to chance. Rakshpal (1960) obtained the areas ofthe dorsal field, harp,and mirror of G. veletis and G. pennsylvanicus by taking measurements of length and width using an oculometer. He said that (p. 501) ... "the size of the mirror is in many cases more or less directly proportional to the size of the tegmen." In the next paragraph, he stated that the size of harp and mirror appeared to be directly proportional to the size of tegmen. No data were given.

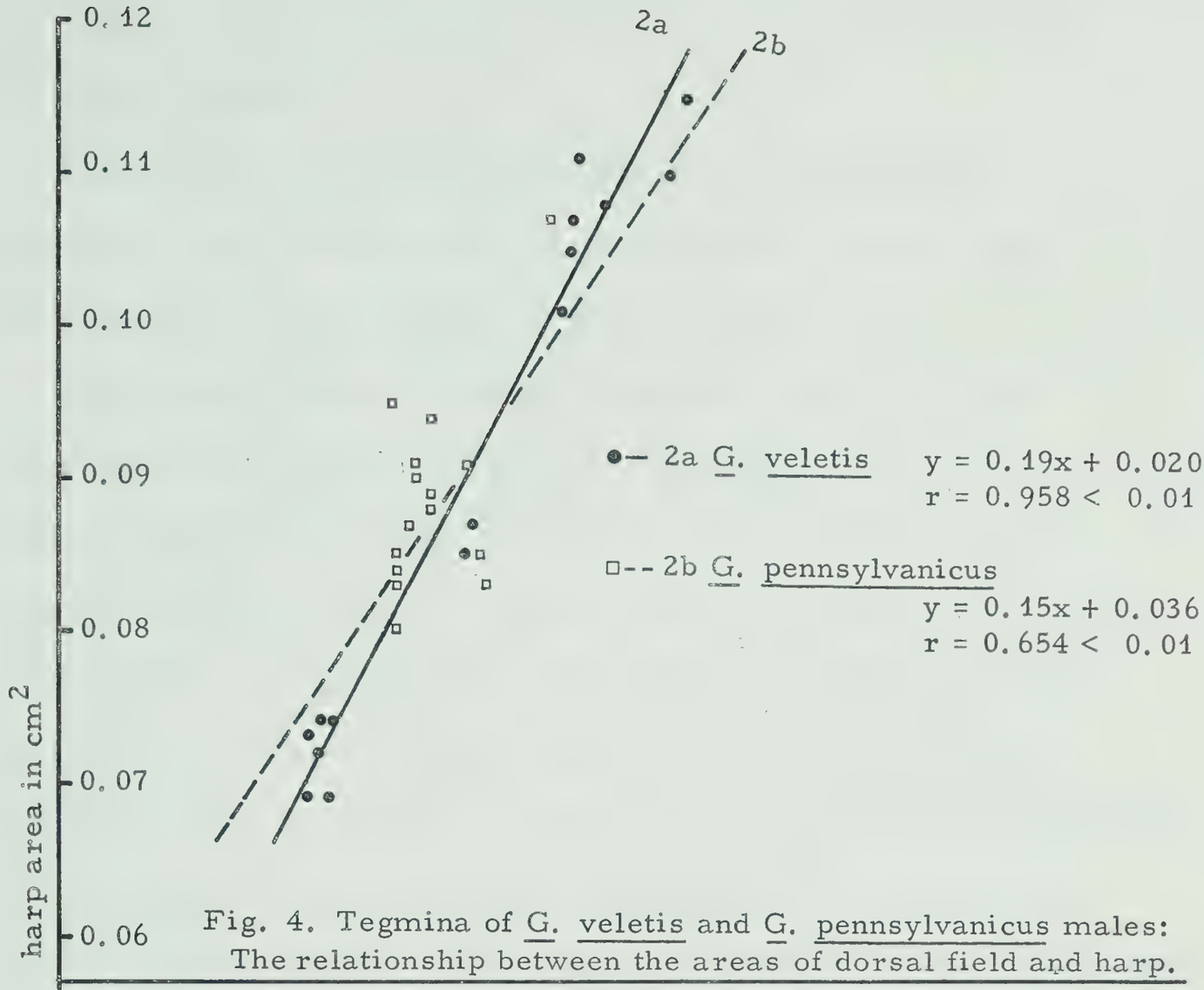



Fig. 4. Tegmina of G. veletis and G. pennsylvanicus males: The relationship between the areas of dorsal field and harp.

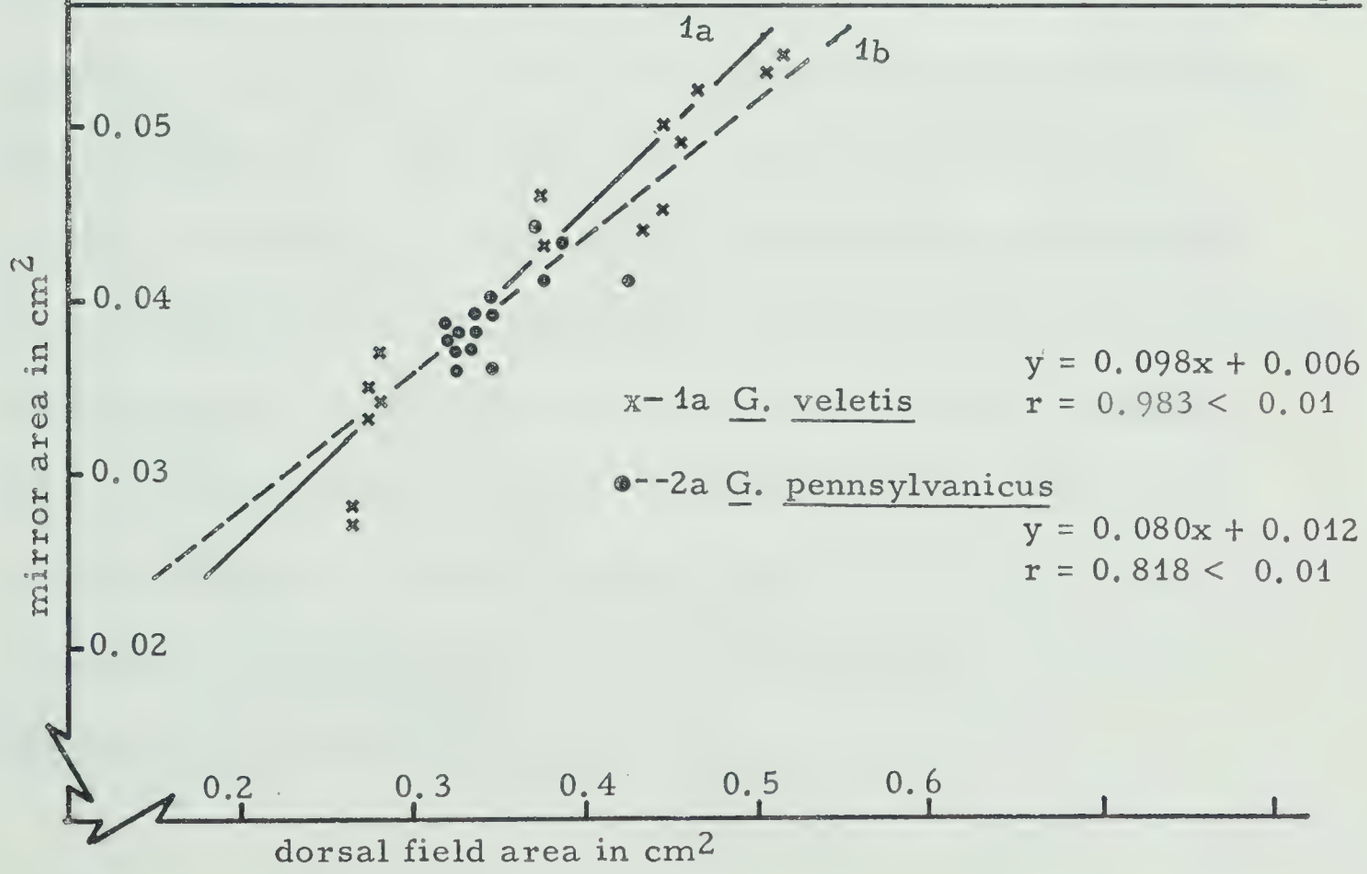



Fig. 5. Tegmina of G. veletis and G. pennsylvanicus males: The relationship between the areas of dorsal field and mirror.

3.12 Venation

The nomenclature used here is that of Comstock (1918). The description of the venation applies to the tegmina of both G. veletis and G. pennsylvanicus, and can be followed on fig. 6.

The costa is either absent or incorporated into the subcosta. The subcosta lies well behind the anterior margin; its accessory branches support most of the lateral field. The unbranched radius runs just behind the subcosta, and the media, its branches supporting the median fan, lies behind the radius. The cubitus divides near the base into $Cu_1$ and $Cu_2$. $Cu_1$ parallels the media to the base of the median fan, then divides into a number of accessory branches supporting the apical area, delimiting the mirror, and forming the boundary between the harp and the cordal area. $Cu_2$ bends abruptly towards the hind tegminal margin where it fuses with 1A and then with 2A in the region known as the node. These three veins separate to form the three cords in the cordal area, with $Cu_2$ and 1A forming an enclosed loop. 3A runs closely behind 2A, reaching the posterior tegminal margin just before the node. Cross veins occur in the lateral field, basal area, and cordal area, but the most strongly developed ones are the three or four forming the "strings" of the harp and the one in the mirror. The veins in the apical area are colored black as cross veins and branches of $Cu_1$ are indistinguishable.

color code for venation:

subcosta - yellow

radius - red

media - blue

cubitus 1 - green

cubitus 2 - lime green

1 anal - orange

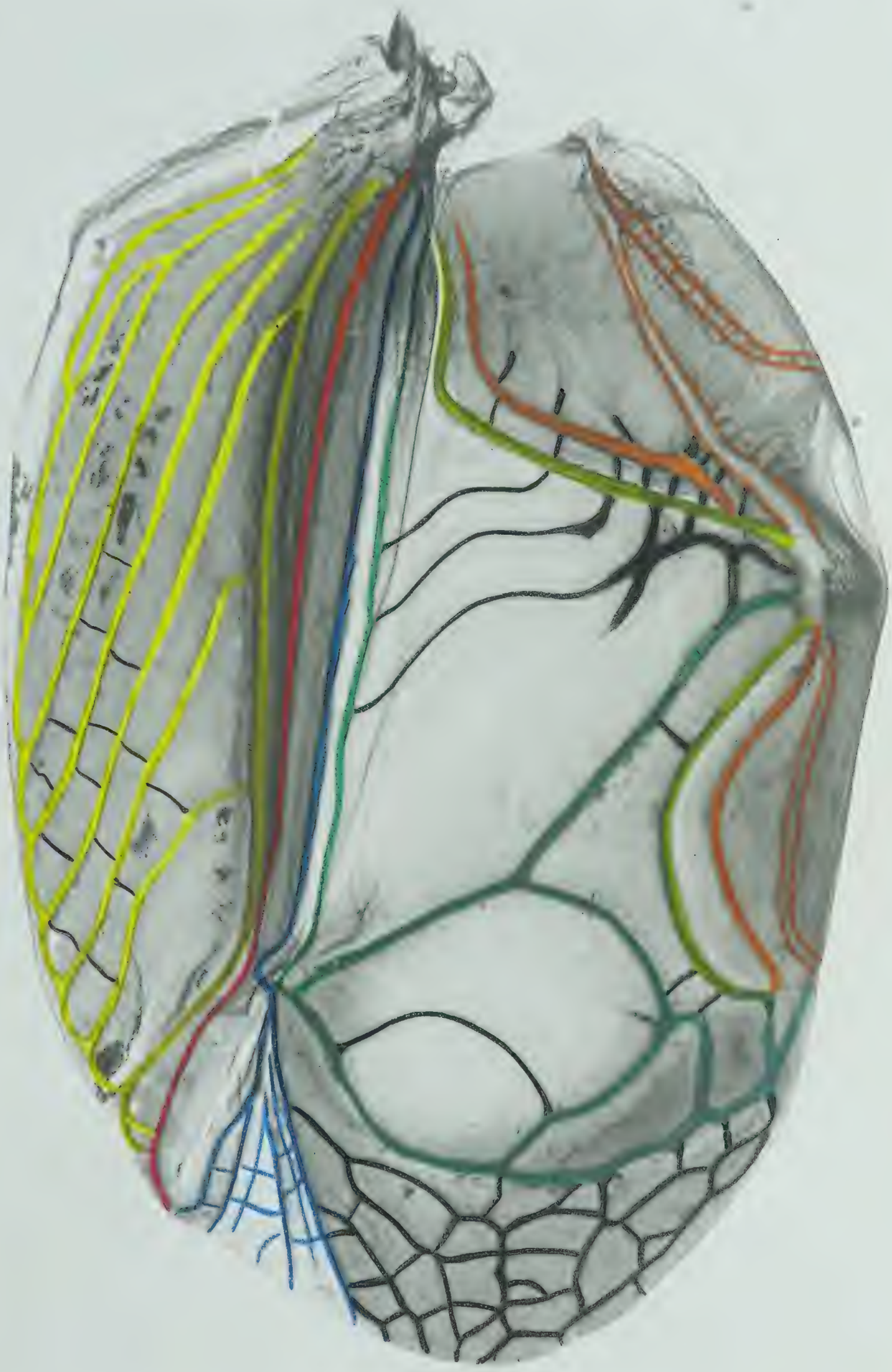
2 anal - open orange

3 anal - hatched orange

cross veins - black

Fig. 6. Venation of the left tegmen of a G. pennsylvanicus male.

X 20



3.13 Sound producing apparatus

The sound producing apparatus is on the dorsal field. The "scraper" is located on the hind margin of the tegmen in the basal area, and the L-shaped "file" is the portion of $Cu_2$ bearing teeth that project ventrally and mesally. This portion of $Cu_2$ lies in a transverse furrow. The mirror and the harp are the main auxiliary structures. The tegmina mounted on the slides mentioned above were photographed again, this time through a microscope, and partial enlargements were printed to give a total magnification of 192. Data pertaining to the file and teeth were obtained from these photographs.

Figure 7, showing the relationship between dorsal field area and file length, and fig. 8, showing the relationship between file length and number of file teeth, were plotted from the data in table 4.

For G. veletis, file length increased linearly with an increase in dorsal field area ($r = 0.778 < 0.01$). For G. pennsylvanicus, there was an increase in file length with an increase in dorsal field area, but from the graph, it appears that the relationship followed a negative concave curve rather than a straight line ($r = 0.500 > 0.05$). The mean dorsal field area was 0.029 $cm^2$ greater for G. veletis than for G. pennsylvanicus, but the mean file length was 0.012 cm longer for G. pennsylvanicus than for G. veletis.

For both species there was an increase in number of teeth with an increase in file length (fig. 8), however, since $r = 0.461 > 0.05$

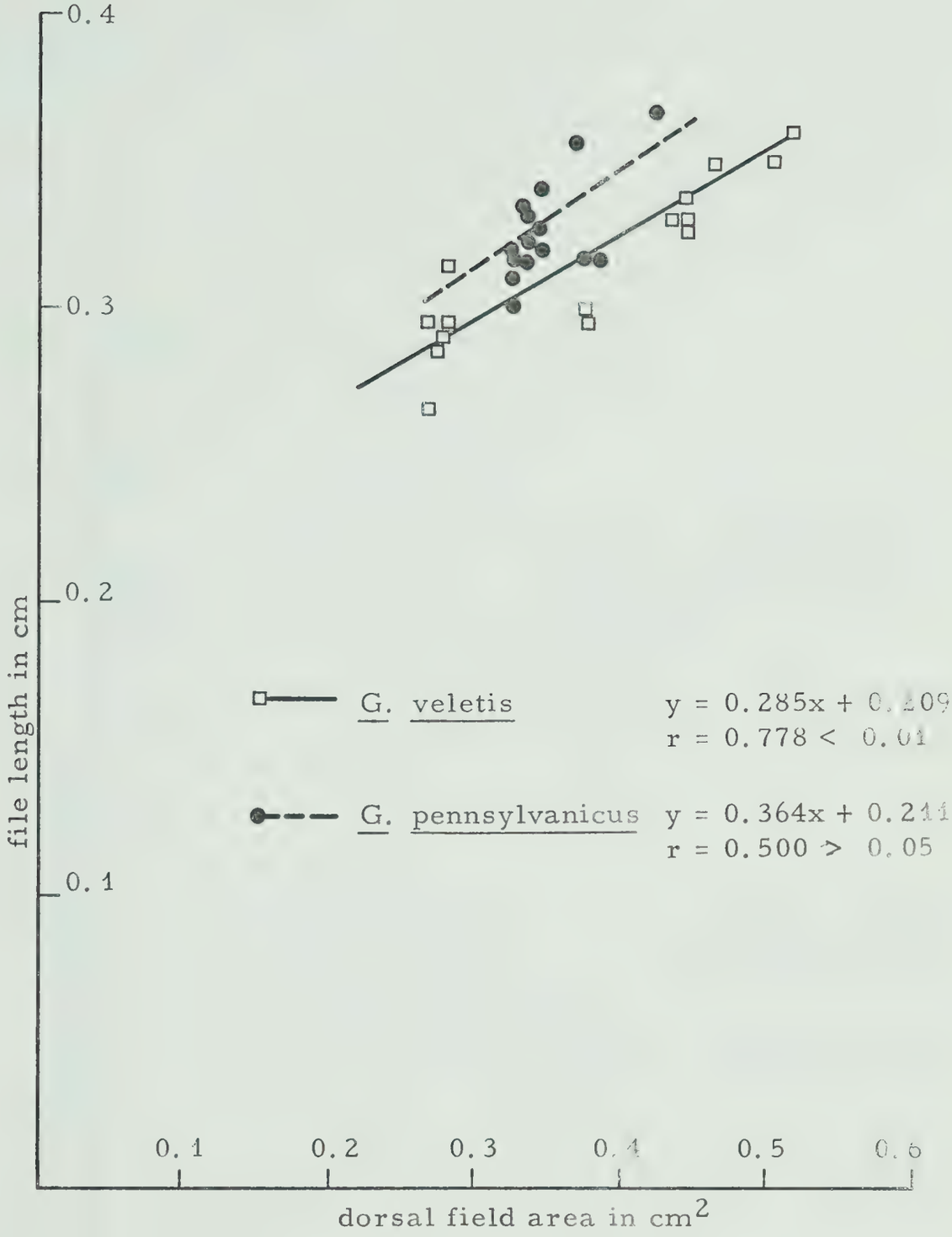



Fig. 7. Tegmina of G. veletis and G. pennsylvanicus males: The relationship between dorsal field area and file length.

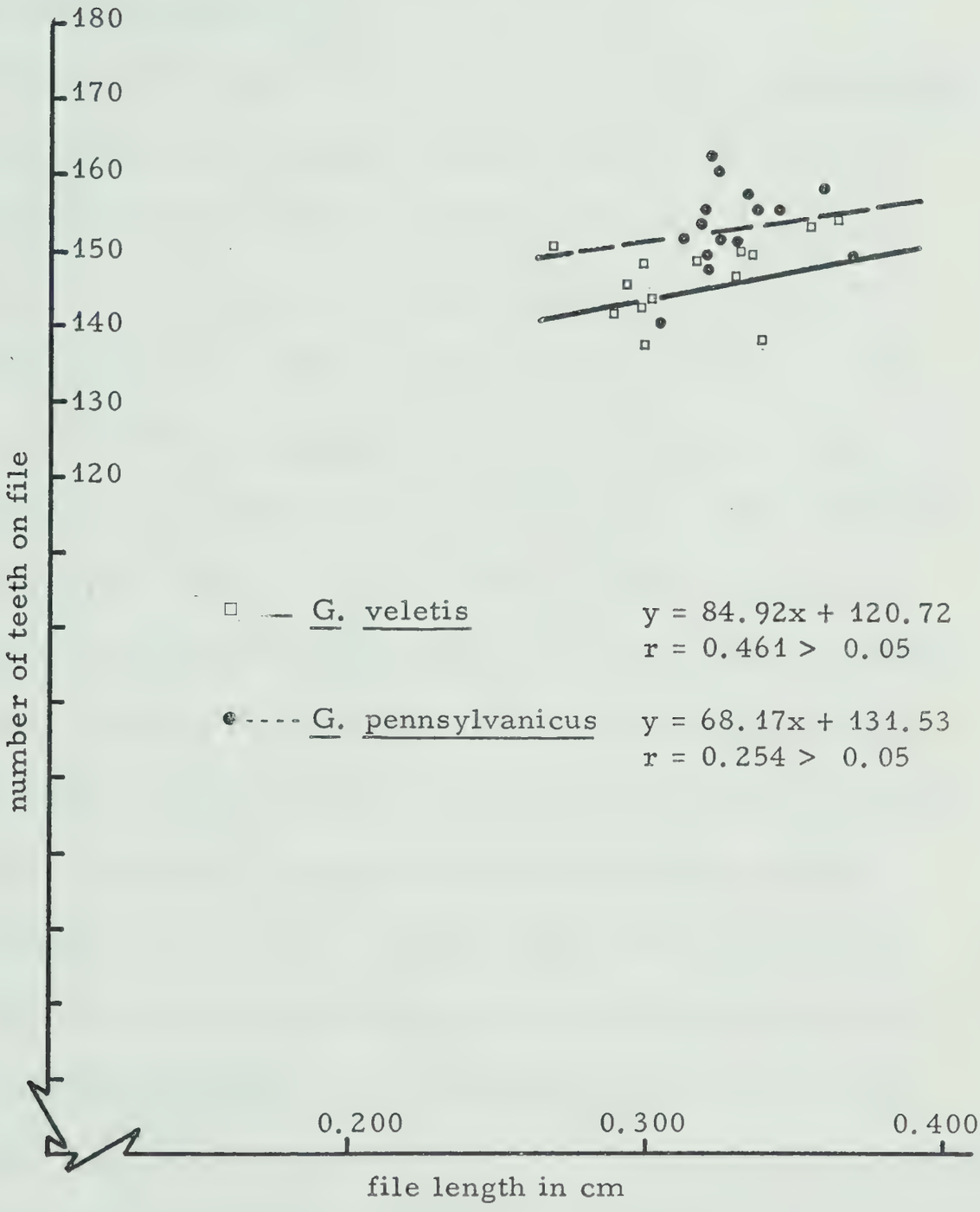



Fig. 8. Tegmina of G. veletis and G. pennsylvanicus males: The relationship between file length and number of file teeth.

and $r = 0.254 > 0.05$ for the regression lines of G. veletis and G. pennsylvanicus respectively, there were more than five chances in a hundred that a linear relationship between number of teeth and file length was due to chance. The mean number of teeth on the file was $147 \pm 5.3$ (range 138-155) for G. veletis and $153 \pm 5.6$ (range 141-163) for G. pennsylvanicus.

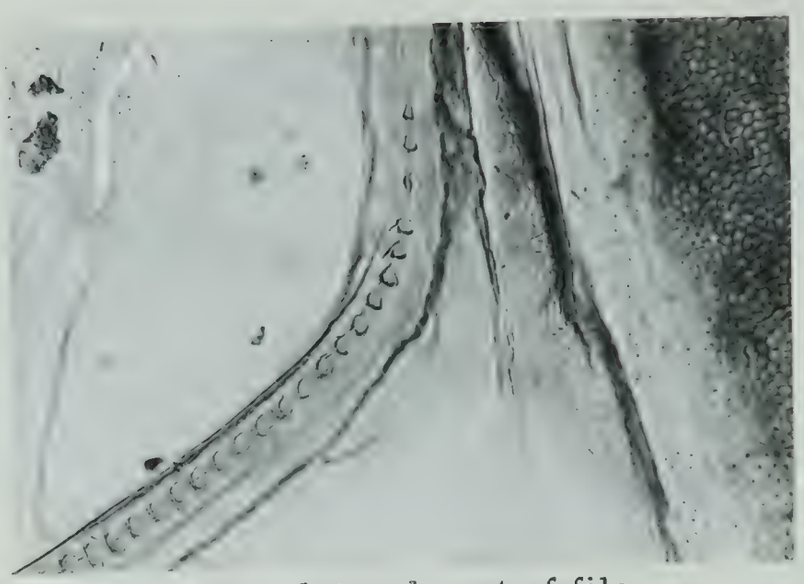
According to Rakshpal (1960), when the tegmina of two individuals are of the same size and the number of teeth varies, the length of the file is directly proportional to the tooth number. He found the mean tooth number to be $143 \pm 11$ for G. veletis (N = 50) and $162 \pm 9$ for G. pennsylvanicus (N = 50). Bigelow (1960) gave the mean tooth number as $138 \pm 10$ for G. veletis (N = 21). The number of teeth can be used to distinguish between some species (Pierce, 1948; Alexander and Thomas, 1957; Rakshpal, 1960; Bigelow, 1960; Leroy, 1962), however with G. veletis and G. pennsylvanicus, tooth number overlaps so much that it is poor as a taxonomic character (Rakshpal, 1960).

The means on tables 5 and 6, which compare the right and left tegmina of G. veletis and G. pennsylvanicus respectively, show that for both species file length, number of file teeth, and the areas of dorsal field and mirror did not differ significantly between the left and right tegmina. The mean areas of the harp for the right and left tegmina were equal for G. veletis, but differed slightly for G. pennsylvanicus. The file teeth on the right and left tegmina appeared equally well developed.

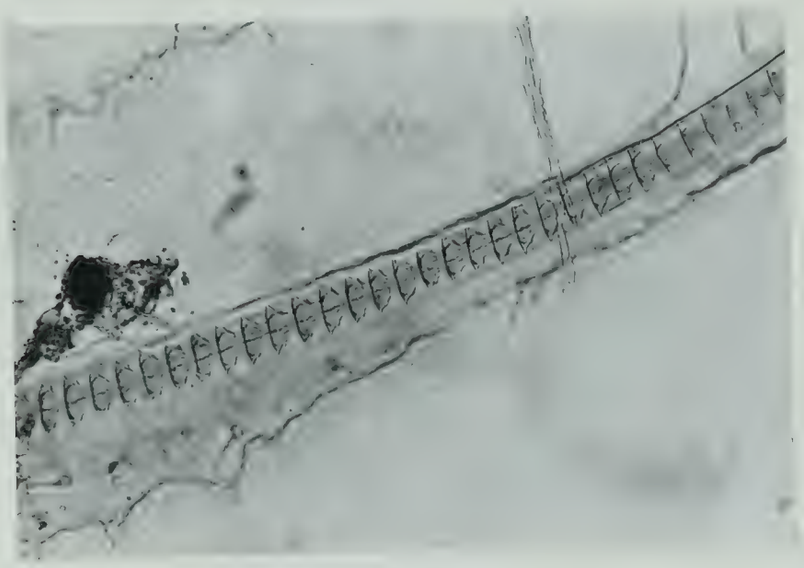
Rakshpal (ibid.) found that the right and left tegmina of G. veletis and G. pennsylvanicus were usually similar in size, the length of the file and the size of the mirror sometimes differed, and the number of file teeth was usually different. In other respects he found the sound producing apparatus of both tegmina to be similar. Pierce (1948) found that the file on the left tegmen of G. assimilis was usually less well developed than the file on the right tegmen.

Rakshpal (1960) separated the file teeth into three groups: small, elliptical teeth on the lateral part of the file; large, elongated teeth on the middle part; and the smallest, though still elongated teeth on the medial part of the file. Figures 9 and 10 show the three groups of file teeth for G. veletis and G. pennsylvanicus respectively. The teeth on the lateral part of the file appear more elliptical for G. pennsylvanicus than for G. veletis, but the two other groups of teeth appear similar for both species. According to Rakshpal and Bigelow (1960), the general size and shape of the file teeth differ amongst congeneric species. Rakshpal showed that for G. pennsylvanicus, the teeth on the lateral part of the file are more elongated, the teeth on the middle part of the file are not as curved, and the teeth on the medial part of the file are more elliptical than the corresponding three groups of teeth for G. veletis.

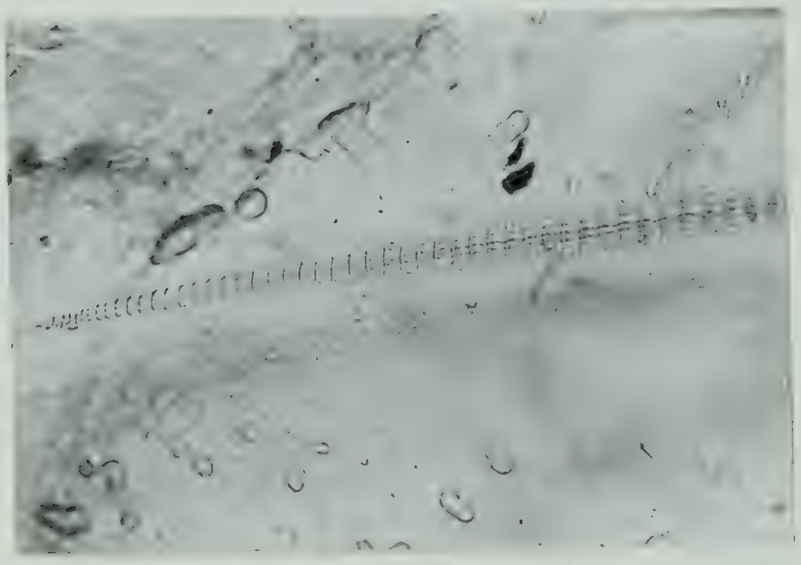
Figure 11, plotted from the data in tables 7 and 8 for G. veletis and G. pennsylvanicus respectively, shows the percentage of the total



a. lateral part of file

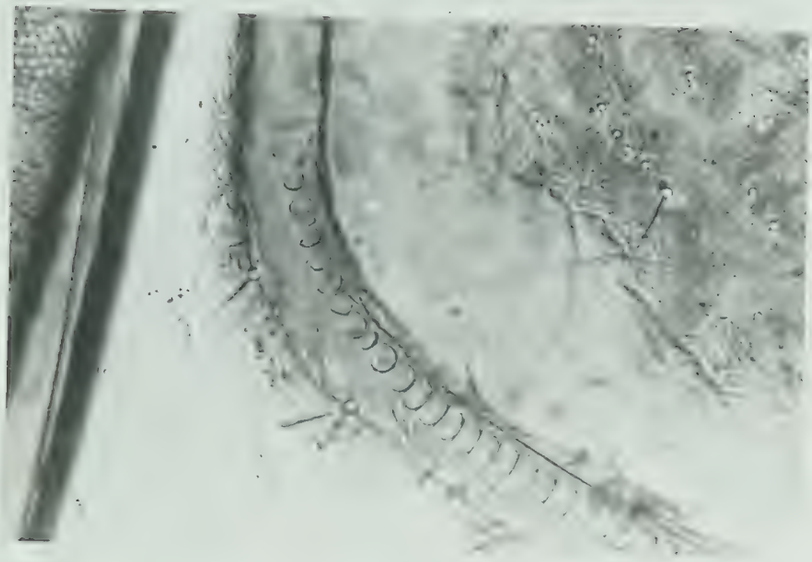


b. middle part of file

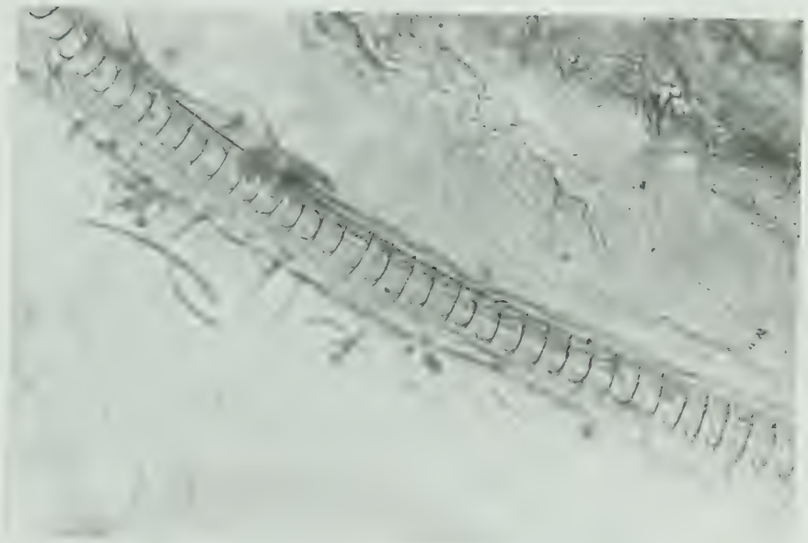


c. medial part of file

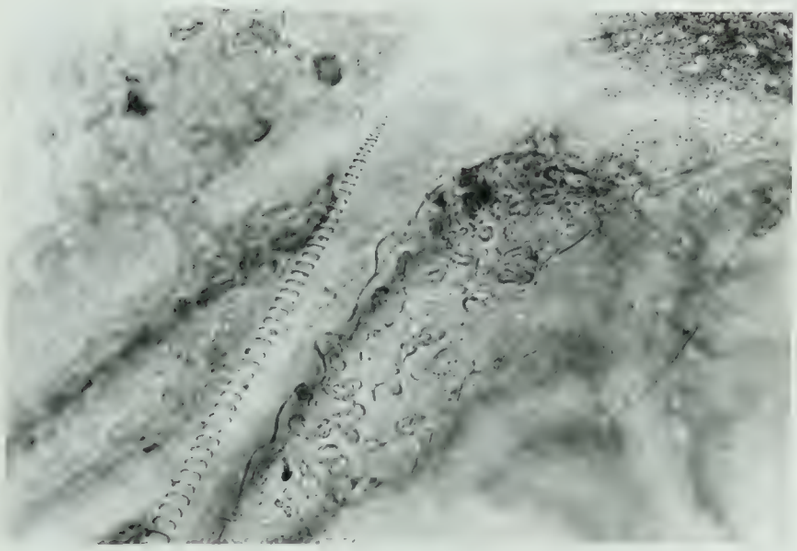
Fig. 9. Left tegmen of a G. veletis male: The three groups of file teeth. X 76 (Ventral view)



a. lateral part of file



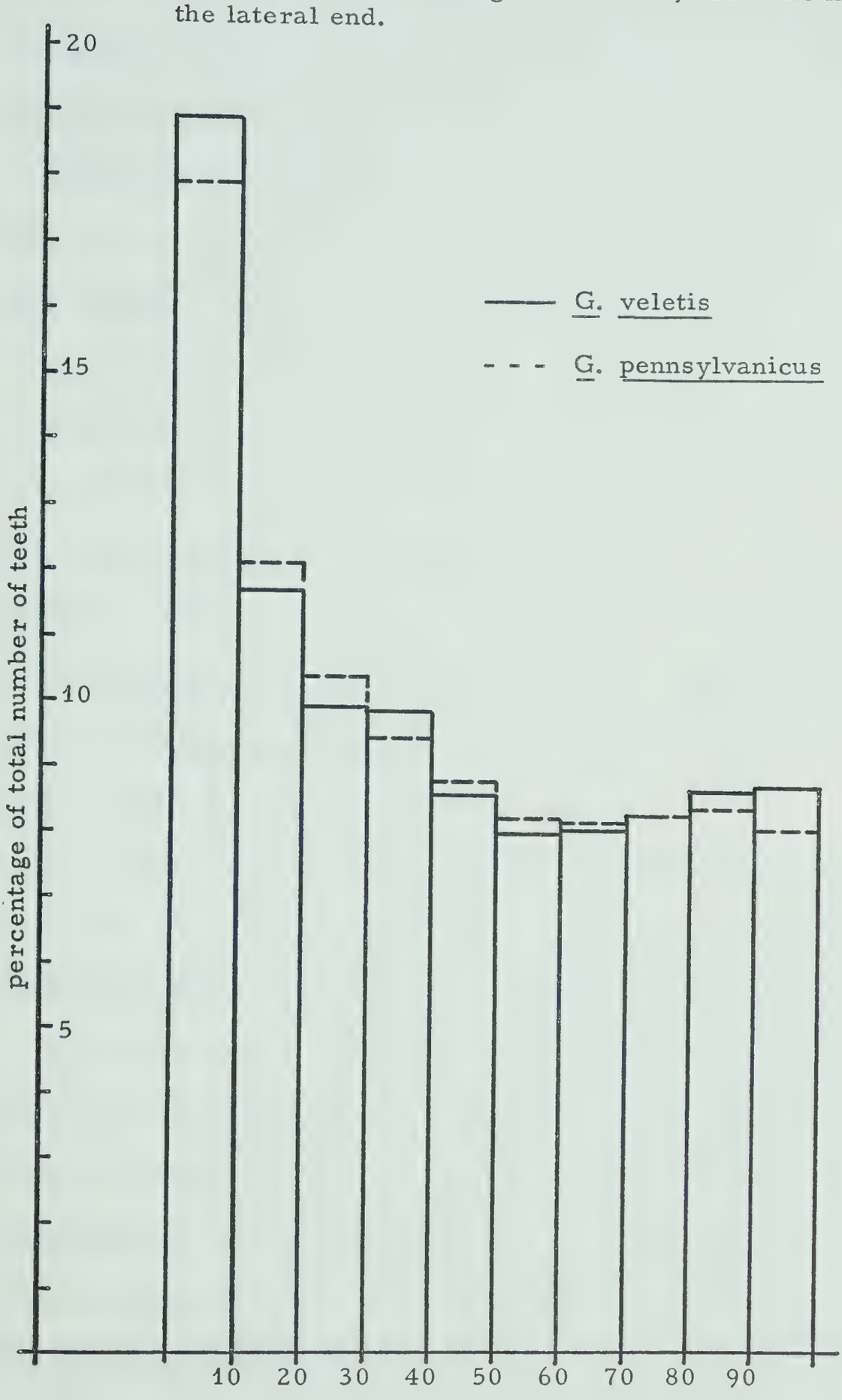
b. middle part of file



c. medial part of file

Fig. 10. Right tegmen of a G. pennsylvanicus male: The three groups of file teeth. X 76 (Ventral view)

Fig. 11. Tegmina of G. veletis and G. pennsylvanicus males: The percentage of the total number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end.



number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end, for both species. For G. veletis, the percentage of teeth decreased progressively from 18.85 to 8.01% from the first to the sixth 10% of the file, then increased progressively up to 8.76% in the last 10% of the file. For G. pennsylvanicus, the percentage of teeth decreased progressively from 17.85 to 8.23% from the first to the seventh 10% of the file, then increased slightly, and finally fell to 8.11% in the last 10% of the file. In both species, the greatest decrease in the percentage of teeth fell between the first and second 10% of the file. Alexander and Thomas (1959) found that although the number of file teeth differed between Nemobius allardi Alexander and Thomas, Nemobius tinnulus Fulton, and Nemobius fasciatus (DeGeer), the distribution of file teeth along the file was similar for all three species.

In order to find out if it was possible for the scraper to make contact with all of the teeth on the file, I traced the ten photographic prints of the right and left tegmina of G. veletis and G. pennsylvanicus on transparent plastic, and marked the positions of the scraper and the file. The transparency of each right tegmen was placed over the transparency of the left tegmen from the same specimen in the normal flexed position. Both were tacked onto a sheet of paper at the position of the second axillary sclerite, so that they could be moved as in life. This was marked off in degrees to facilitate checking that the right and left transparencies were opened and closed by the

same amounts. In neither species could the scraper make contact with about 10 of the lateral teeth on the file because the left tegmen was prevented from moving further mesad by striking the perpendicular junction between the lateral field and the dorsal field of the right tegmen.

## 3.2 Calling songs

### 3.21 Description of a chirp

The calling songs of G. veletis and G. pennsylvanicus are composed of chirps, and there was no difference between the sounds of these two species. There was no noticeable difference in either species in their readiness to chirp as the relative humidity varied between 30% and 40% or with changes in light intensity. Below 20 C chirping became very sporadic.

According to Alexander's (1962) classification of the chirping rhythm pattern (see section 1.0), G. veletis and G. pennsylvanicus have chirps of intermediate length, delivered at intermediate rates, and somewhat irregularly. A detailed study of the effect of temperature on chirp rate is feasible only with species that are regular chirpers (Walker, 1962), therefore I did not study the chirp rate. The duration of a chirp depended on the number of pulses per chirp and the pulse rate.

The number of pulses per chirp varied from three to six for G. veletis and from three to four for G. pennsylvanicus (table 9). Both species are reported to have three, four, and five-pulsed chirps (Alexander and Bigelow, 1960). G. veletis sometimes has six and seven-pulsed chirps, the mode being a four-pulsed chirp (Alexander, 1957b). The frequency distribution of pulse numbers in a chirp may be a useful taxonomic reference (Leroy, 1962).

One or two faint, short marks sometimes appeared on the sonagrams at the beginning of a chirp (fig. 1). Table 10 shows the percentage of sonagram chirps beginning with these marks. According to Lutz and Hicks (1930), they could represent separate pulses or merely be an interrupted first pulse. They were not included in any of my measurements.

All pulses appeared to have the same intensity. At six inches from Gryllus species, the intensity of the song is 70-100 db (Alexander, 1966). The leading edge of every pulse was more sharply demarkated than the trailing edge.

The means of the grand average pulse durations for the first three pulses within a chirp and the means of the grand average pulse intervals are given in table 11 at 24.9 C for G. veletis and in table 12 at 26.3 C for G. pennsylvanicus. Pulse duration increased progressively from 11.86 m sec for the first pulse to 17.51 m sec for the third pulse for G. veletis, and from 13.97 m sec for the first pulse to 19.20 m sec for the third pulse for G. pennsylvanicus. The first pulse was of much shorter duration than the following pulses in both species. The means of the grand average pulse intervals between these first three pulses increased from 21.60 to 23.86 m sec for G. veletis and from 24.95 to 28.43 m sec for G. pennsylvanicus. The ratio of the average pulse interval to the average pulse duration was 1.54 for G. veletis and 1.59 for G. pennsylvanicus.

There is no data in the literature on pulse duration or pulse interval for these two species. For G. assimilis, Pierce (1948) and Lutz and Hicks (1930) found a progressive increase in pulse duration from the beginning to the end of a chirp, with the first pulse of much shorter duration than the following pulses. The pulse intervals were very constant. Pierce found the ratio of pulse interval to pulse duration to be 1.70. According to Lutz and Hicks, it was 0.89. These authors did not give the temperatures at which their data were obtained. At 25 C, Leroy (1962) found that pulse duration was greater than pulse interval for Gryllus peruviensis Saussure, less than pulse interval for Gryllus argentinus Saussure, and about equal to pulse interval for Gryllus capitatus Saussure. She also found that the first pulse within a chirp was usually of shorter duration than the following pulses.

Data on dominant frequency for G. veletis specimens #4 and #6 are not included in table 13 because the sonagrams were too poor for these measurements to be made. Dominant frequency decreased from the beginning to the end of each pulse, but decreased at a faster rate at the beginning of the pulse than towards the end of the pulse. This agrees with Walker's (1962) finding. The means of the grand average dominant frequencies for the first three pulses, given in table 13 at 25.2 C for G. veletis and in table 14 at 26.3 C for G. pennsylvanicus, show that dominant frequency of the first pulse

was much lower than dominant frequency of the following pulses within the chirp. For G. veletis, there was a progressive increase in dominant frequency of the pulses within a chirp from 4.34 kcps for the first pulse to 4.49 kcps for the third pulse. For G. pennsylvanicus, dominant frequency increased from 4.05 kcps for the first pulse to 4.14 kcps for the second and third pulses.

The number of teeth struck per pulse was calculated by multiplying the dominant frequency in cps by the duration of the pulse in seconds. These calculations were only made for G. veletis as data on dominant frequency and pulse duration for G. pennsylvanicus was questionable because of the recording technique described previously. The means of the number of teeth struck during the first three pulses, shown in table 17 at 25.2 C, increased progressively from 52.04 for the first pulse to 77.65 for the third pulse, with the first pulse having many fewer teeth struck than the second and third pulses. Leroy (1962) found that within a chirp, it was rare that the number of teeth struck per pulse was the same for different pulses.

3.22 Effect of temperature change on pulse rate

Pulse rates ranged from 14.9 to 36.9 pulses/sec for G. veletis, and from 20.1 to 25.2 pulses/sec for G. pennsylvanicus (tables 15 and 16 respectively), with warmer crickets producing faster pulse rates than colder crickets (fig. 12). The correlation coefficients for the regression lines are $0.916 < 0.01$ for G. veletis and $0.439 > 0.05$ for G. pennsylvanicus. For G. veletis, a sigmoid can be drawn between 10 C and 45 C (fig. 12). There is no data on temperature versus pulse rate for G. pennsylvanicus in the literature. At 29.4 C, Alexander (1957a) gave the mean pulse rate for G. veletis as 25.0 with a range between 24.0 and 29.0 pulses/sec. My calculations from the equation of the regression line show that at 29.4 C, the pulse rate would be 31.2 pulses/sec for this species. Walker (1962) plotted temperature against pulse rate for 20 cricket species representing seven genera and five subfamilies. The relationship was always linear with warmer crickets producing faster pulse rates than colder crickets.

When the regression lines are extrapolated downwards, zero pulses/sec occur at -1.47 C for G. veletis and -44.64 C for G. pennsylvanicus. Walker (ibid.) found that regression lines tended to converge at -4.0 C and zero pulses/sec, with a range between 0.6 C and 7.7 C, and he suggested that this tendency to converge might be more pronounced with more accurate or more extensive data. Crickets usually sing only between 10.0 C and 45.0 C (Alexander, 1960).

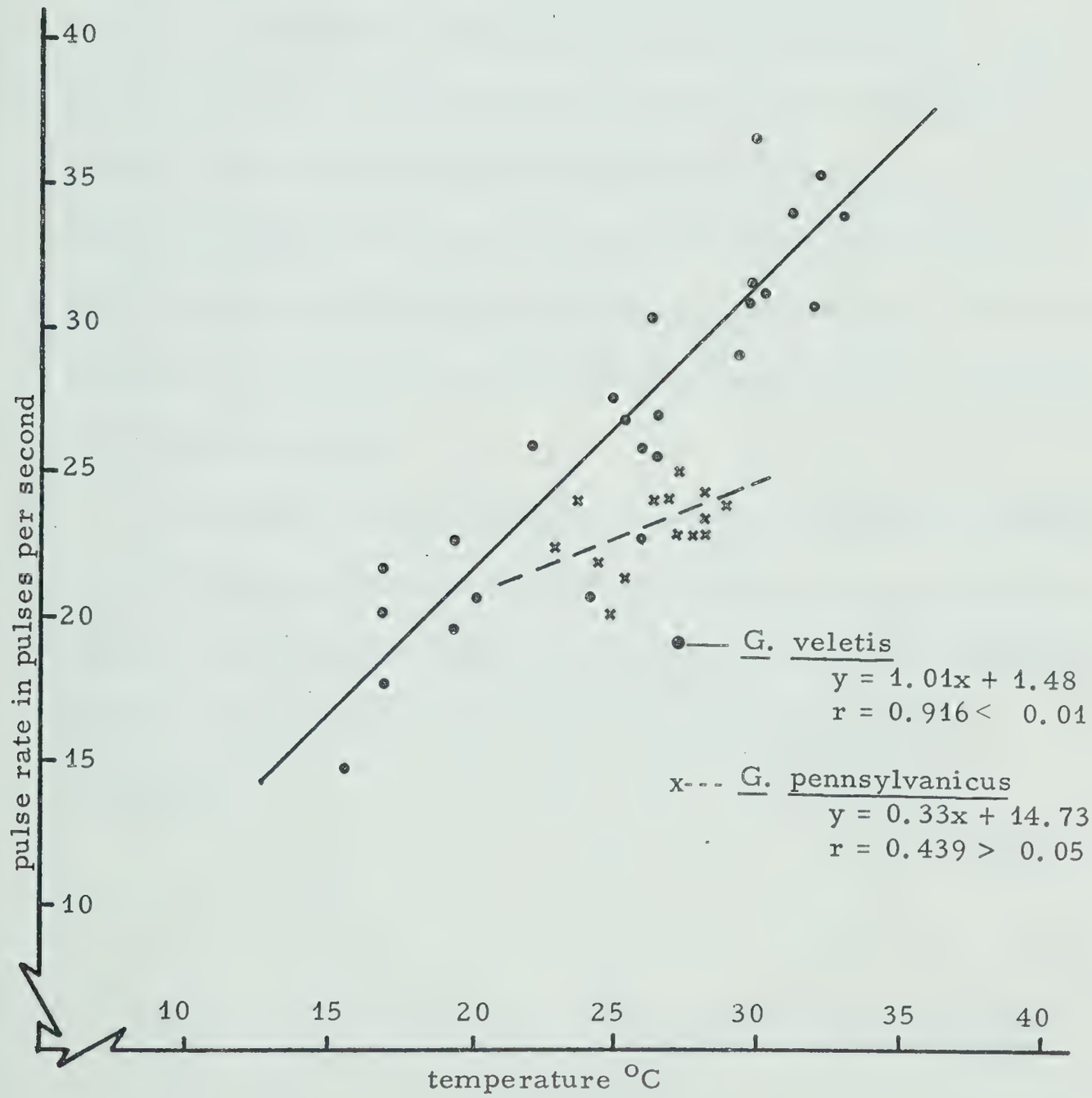



Fig. 12. G. veletis and G. pennsylvanicus calling songs: The relationship between temperature and pulse rate.

3.23 Effect of temperature change on pulse duration and pulse interval

Figure 13, showing the relationship between temperature, pulse duration, and pulse interval, was plotted from the data in tables 11 and 12 for G. veletis and G. pennsylvanicus respectively. For G. veletis, pulse duration and pulse interval decreased linearly with an increase in temperature ($r = 0.603 < 0.01$ for pulse duration and $0.877 < 0.01$ for pulse interval). Pulse interval decreased 3.85 fold faster than pulse duration for a unit increase in temperature. At 34.5 C pulse interval and pulse duration would be equal. For G. pennsylvanicus, pulse duration and pulse interval did not appear to follow a definite pattern with an increase in temperature. The difficulty encountered in measuring sonagrams of chirps recorded in gallon jars could account for this.

There is no published data on the relationship between temperature, pulse duration, and pulse interval for G. veletis or G. pennsylvanicus. Walker (1962) said that with all the crickets he studied, pulse interval always decreased faster than pulse duration with an increase in temperature.

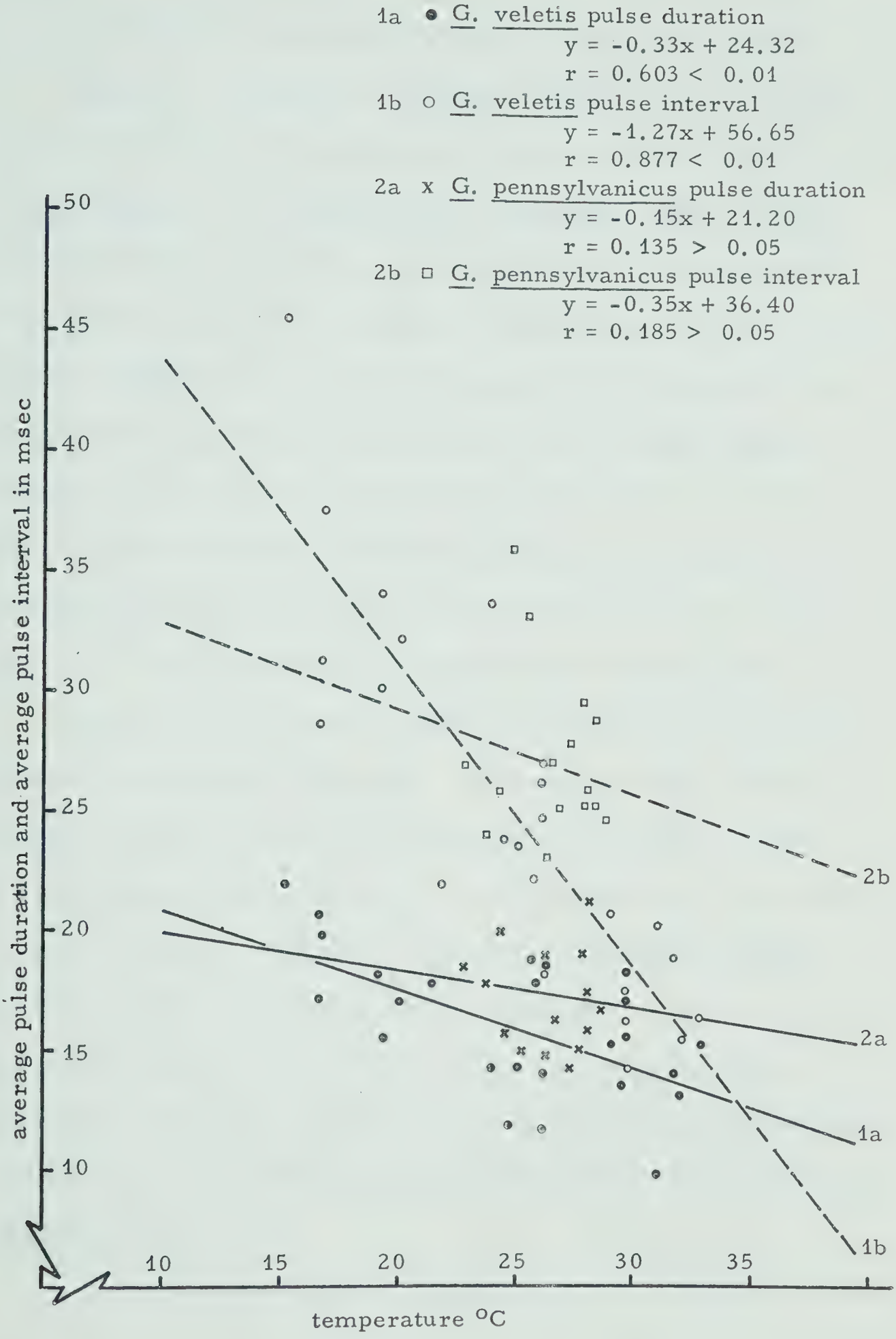



Fig. 13. G. veletis and G. pennsylvanicus calling songs: The relationship between temperature, pulse duration, and pulse interval.

3.24 Effect of temperature change on dominant frequency

Figure 14, showing the relationship between temperature and dominant frequency, was plotted from the data in tables 13 and 14 for G. veletis and G. pennsylvanicus respectively. For G. veletis, dominant frequency of a chirp ranged from 3.99 to 5.37 kcps and increased linearly with an increase in temperature ($r = 0.603 < 0.01$). For G. pennsylvanicus, dominant frequency of a chirp ranged from 3.63 to 4.54 kcps, but did not appear to have a definite pattern with an increase in temperature. The individual data for the four specimens whose calling songs were recorded at more than one temperature shows that dominant frequency increased with temperature in two specimens (#27, #33), but decreased in the other two specimens (#4, #2).

Alexander (1966) found that field cricket chirps had a dominant frequency of from four to five kcps. According to Walker (1962), dominant frequency increased as temperature increased, at least at low and moderate temperatures (10 - 25 C), but the exact relationship varied from species to species. The rate of increase in dominant frequency with temperature sometimes decreased or became zero. If the rate of change was very low, only by following the data for individuals was a rise in dominant frequency with temperature demonstrated. He knew of no way to predict the shape of the curve even if all the other relationships were known.

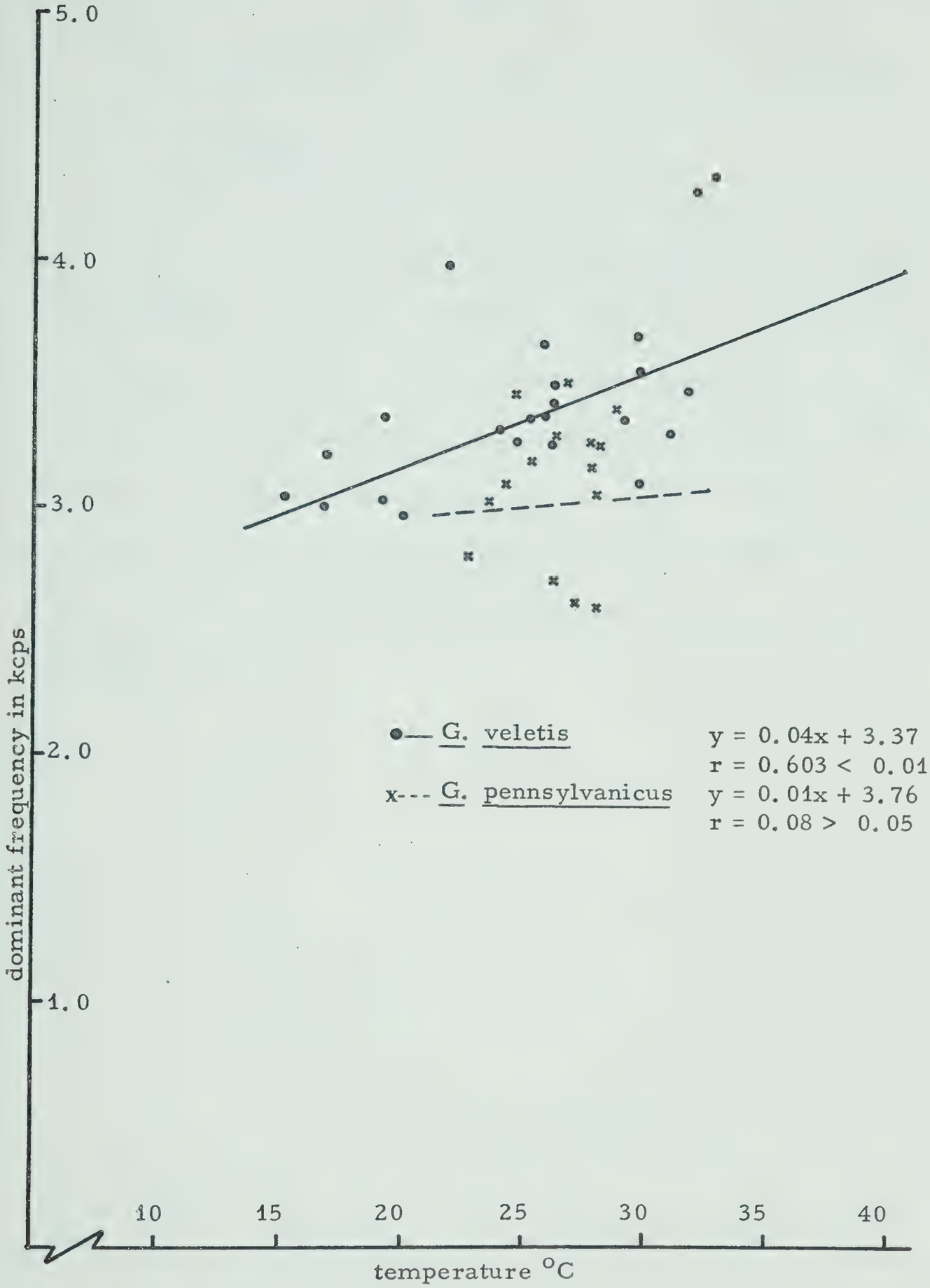



Fig. 14. G. veletis and G. pennsylvanicus calling songs: The relationship between temperature and dominant frequency.

3.25 Effect of temperature change on number of teeth struck per pulse

As was mentioned under the description of a chirp, the number of teeth struck per pulse was obtained for G. veletis by multiplying the dominant frequency by the duration of the pulse. Within a chirp, the average number of teeth struck per pulse ranged from 43.5 to 90.1 (table 17), but fig. 15 does not show a discernible pattern relating number of teeth struck per pulse and temperature. Walker (1962) found that in some species there was a reduction in number of teeth struck per pulse as the temperature increased, but in other species, there was no such reduction.

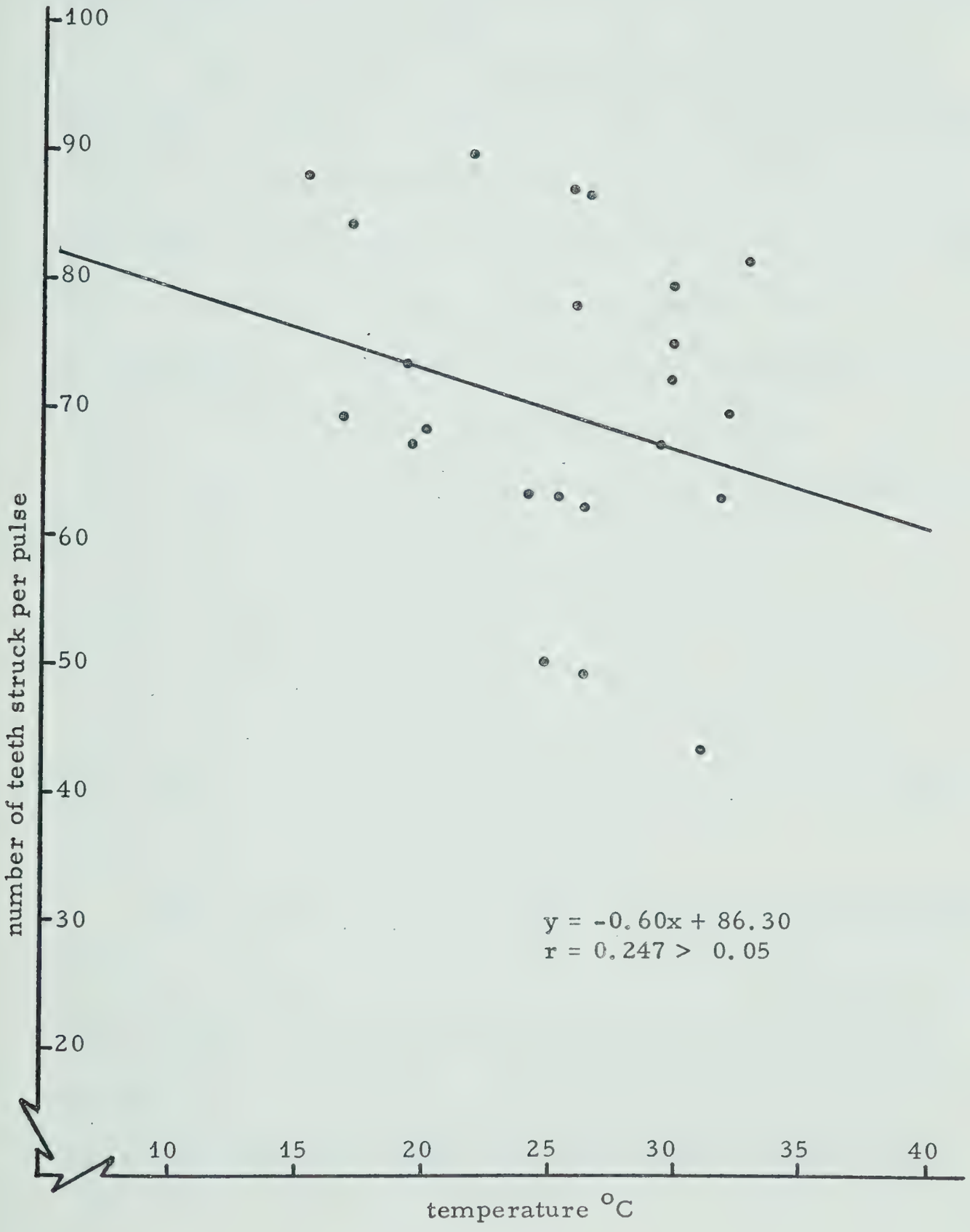



Fig. 15. G. veletis calling song: The relationship between temperature and number of teeth struck per pulse.

## 4.0 DISCUSSION

Rakshpal (1960) and Huber (1962) took crickets that had the right tegmen over the left tegmen (R/L) and changed them to a L/R position before the chitin of their tegmina had hardened after the final moult. Most of the crickets reverted to the R/L position within 24 hours. Rakshpal found that crickets that retained the L/R position sang softer than was normal for the first one to three days, but eventually they produced a normal song. According to Huber, specimens of G. campestris which retained the L/R position always produced sounds which had a lower intensity, broader frequency spectrum, to some extent irregular pulse intervals, and fewer tooth strikes per pulse than the sounds produced by crickets that retained an initial R/L or L/R tegminal position. Communication between males with the new L/R tegminal position and females appeared normal. He concluded that since the stridulatory organs were symmetrically constructed, these differences in sound indicated a slight asymmetry in the function of the effector organs (muscles and nerves).

When Rakshpal (1960) and Walker (1962) punctured or removed the harp or mirror, a softer, but otherwise normal, song was produced. They concluded that the function of these areas was to increase the intensity of the song. The fact that the file teeth project mesad so that the scraper moves "against the grain" during sound production

probably increases the amplitude of vibration of the tegmina, producing a more intense sound (Pierce, 1948).

The fact that $Cu_2$ lies in a transverse furrow makes the teeth more accessible to the scraper.

For G. veletis, the percentage of file teeth struck per pulse ranged from 29.46 to 61.11 (table 17). Kreidl and Regen (1905), Lutz and Hicks (1930), Pierce (1948), Rakshpal (1960) and Leroy (1962) also found that only a fraction of the file teeth were struck per pulse. The question that arises, is which part of the file is used. I explained previously that about 10 of the lateral teeth on the file could not be struck in G. veletis and G. pennsylvanicus. There may be relatively few of the remaining teeth that are never used. For G. veletis, as many as 90 teeth were struck per pulse, and assuming that all of the medial teeth were struck, this would involve slightly over one half of the file. Different groups of teeth may be used for different pulses and also for different songs. Kreidl and Regen (1905) tried to determine which part of the file was used by G. campestris by greasing the file and seeing where the grease remained after chirping stopped. They concluded that only a few teeth at each end of the file were not used. Rakshpal (1960) pressed the thorax of specimens of G. assimilis and G. veletis to raise their tegmina, then let the tegmina move inwards either by themselves or assisted by his thumb. He concluded that only the medial one third of the file was struck per pulse because

the left tegmen did not move below the right tegmen beyond that point by itself. When made to move further with the aid of forceps, the sound produced was not characteristic of the species. Rakshpal did not describe this artificially produced sound or offer any explanation as to why it should differ from the normal song.

The function, if any, of the unused part of the file is unknown. Rakshpal (1960) suggested that it (p. 506, 507) ... "may further help in producing a specific modulated frequency in a way analogous to what occurs in our stringed instruments, in which only a part of the string is engaged by the bow. When a small peg is put on the string, the modulated quality of the string changes." I do not think that Rakshpal's analogy between the string of a stringed instrument and the file on a tegmen is legitimate. In stringed instruments, the rate of vibration of the string itself determines the frequency of the sound produced. If a peg is placed on the string and the string is plucked on one side of the peg, the string can vibrate in parts as well as as a whole, thus producing a more complex frequency spectrum. The dominant frequency of a cricket sounds is determined not by the vibration of the file as a whole or in parts, but by the number of file teeth struck per second.

For G. veletis at 25.2 C, an average of 4/10 of the file (0.0016 cm) was used per pulse (tables 17 and 7). Assuming that all of the medial teeth were struck, the velocity of tegminal motion ($v = \frac{d}{t}$, where d = distance and t = time) was 1.26 cm/sec when the first quarter of the file

was being struck and 1.38 cm/sec when the last quarter of the file was being struck. (In the formula for velocity, the value of t was calculated for the first quarter of pulse duration and for the last quarter of pulse duration by using the highest frequency and the lowest frequency respectively of the mean frequency range of the pulse, shown in table 13). Therefore,the decrease in dominant frequency from the beginning to the end of a pulse cannot be attributed to a decrease in the speed of tegminal motion. It was solely due to the file teeth being further apart near the lateral end of the file so that the number of teeth struck per second was less towards the end of tegminal closing. Leroy (1962) and Huber (1962) suggested that a lower speed of tegminal motion, and perhaps the gradual change in the shape and size of the teeth,could also help to account for the decrease in dominant frequency within a pulse. Dominant frequency decreased faster at the beginning of the pulse than towards the end of the pulse because the greatest decrease in the percentage of the total number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end, fell between the first and second 10% of the file (fig. 9).

For G. veletis, pulse duration increased progressively within a chirp because the number of teeth struck per pulse increased progressively within the chirp. Dominant frequency also increased progressively from the first pulse to the last pulse within a chirp, and since this would have tended to progressively decrease pulse duration, its effect

must have been outweighed by the progressive increase in the number of teeth struck per pulse. For G. pennsylvanicus, pulse duration increased progressively within a chirp, however, this increase was not due to a progressive decrease in dominant frequency. Dominant frequency increased from the first pulse to the second pulse, which would have tended to make the duration of the second pulse shorter than the duration of the first pulse; dominant frequency was equal for the second and third pulses, which would have tended to make pulse duration equal for the second and third pulses. Therefore, although there is no data on number of teeth struck per pulse for this species, the progressive increase in pulse duration within a chirp must have been due to a progressive increase in the number of teeth struck per pulse within the chirp.

Pulse rate of G. veletis increased with an increase in temperature because both pulse duration and pulse interval decreased. There was no indication that fewer teeth were struck per pulse, so the decrease in pulse duration must have resulted from an increased speed of tegminal closing. The proportion of the tegminal stroke cycle occupied by tegminal closing increased as the temperature increased because pulse interval decreased 3.85 fold faster than pulse duration for a unit increase in temperature. Walker (1962) said that he has not developed a completely satisfactory technique for determining duration or speed of tegminal

opening or closing,or for determining the number of teeth struck per pulse. A mathematical check of the correlation between pulse rate, pulse duration, and pulse interval, using the equations of their regression lines, shows that at 24.9 C, the mean temperature, pulse rate is 26.63 pulses/sec, pulse duration is 16.10 m sec, and pulse interval is 31.62 m sec. The sum of the duration of 26.63 pulses and 25.63 pulse intervals is 1.24 sec, not one sec, giving a 24% error. Perhaps pulse duration and pulse interval did not decrease linearly with an increase in temperature (even though the correlation coefficients for their regression lines were very significant), but more in the pattern of positive concave curves (fig. 13).

Pulse rate of G. pennsylvanicus also increased with an increase in temperature,so pulse duration, pulse interval, or both,must have decreased. Since the slope of the regression line of pulse rate versus temperature was 3.06 fold less for G. pennsylvanicus than for G. veletis, pulse duration, pulse interval,or both,must have decreased at a slower rate for G. pennsylvanicus than for G. veletis.

Above 19.4 C, G. pennsylvanicus had lower pulse rates than G. veletis. This could reflect the fact that on the average, the G. pennsylvanicus file was 0.012 cm longer and had 7.4 more teeth than the G. veletis file. However, amongst closely related species, differences in pulse rates are mainly due to differences in the number of teeth struck

per pulse, differences in tegminal stroke rates, or both, and they are genetically determined (Alexander, 1962; Bigelow, 1964; Alexander, 1966). Differences in sound producing apparatus probably play a minor role in producing song differences between closely related species (Alexander, 1962). Differences in the size and shape of their teeth may cause differences in their songs which have not yet been detected (Rakshpal, 1960). The lower pulse rates of G. pennsylvanicus above 19.4 C are then largely explained by the fact that above 16.5 C pulse duration was greater, and above 22.5 C pulse interval was also greater, for G. pennsylvanicus than for G. veletis (fig. 13).

For G. veletis, pulse rate increased 25.25 fold faster than dominant frequency with a unit increase in temperature. The reason for this is that as pulse rate increased, pulse interval decreased 3.85 fold faster than pulse duration.

In conclusion, at a given temperature, I found that the calling songs of G. veletis and G. pennsylvanicus had different pulse rates. In opposition to my data, neither Bigelow (1960) nor Rakshpal (1960) found any significant differences between the calling songs of these two species. Thus their data supports the evidence that sympatric species whose breeding seasons are seasonally isolated may have identical calling songs (Alexander, 1962).

## 5.0 REFERENCES

ALEXANDER, R. D. 1957a. Sound production and associated behavior in insects. Ohio J. Sci. 57: 101-113.

————————. 1957b. The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: Acheta). Ann. Ent. Soc. Amer. 50: 584-602.

————————. 1960. Sound communication in Orthoptera and Cicadidae, p. 38 to 92. In W. E. Lanyon and W. N. Tavolga [ed.]. Animal sounds and communication. AIBS, Publ. 7, Washington.

————————. 1961. Aggressiveness, territoriality, and sexual behaviour in field crickets. Behaviour 17: 130-223.

————————. 1962. Evolutionary change in cricket acoustical communication. Evolution 16: 443-467.

————————. 1966. The evolution of cricket chirps. Nat. Hist., N. Y. 75(9): 27-31.

ALEXANDER, R. D. and R. S. BIGELOW. 1960. Allochronic speciation in field crickets, and a new species, Acheta veletis. Evolution 14: 334-346.

ALEXANDER, R. D. and E. S. THOMAS. 1959. Systematic and behavioral studies on the crickets of the Nemobius fasciatus group (Orthoptera: Gryllidae: Nemobiinae). Ann. Ent. Soc. Amer. 52: 591-605.

ALLARD, H. A. 1917. Synchronism and synchronic rhythm in the behavior of certain creatures. Amer. Nat. 51: 438-446.

————————. 1929. Physiological differentiation in overwintering individuals of certain musical Orthoptera. Can. Ent. 61: 195-198.

————————. 1930a. The chirping rates of the snowy tree crickets (O. niveus) as affected by external conditions. Can. Ent. 62: 131-142.

————————. 1930b. Changing the chirp rate of the snowy tree cricket Oecanthus niveus with air currents. Science 72: 347-349.

BESSEY, C. A. and E. A. BESSEY. 1898. Further notes on thermometer crickets. Amer. Nat. 32: 263-264.

BIGELOW, R. S. 1960. Interspecific hybrids and speciation in the genus Acheta (Orthoptera, Gryllidae). Can. J. Zool. 38: 509-524.

————————. 1964. Song differences in closely related cricket species and their significance. Aust. J. Sci. 27(4): 99-102.

BROOKS, M. W. 1881. Influence of temperature on the chirp of the cricket. Pop. Sci. Monthly 20: 268.

BROUGHTON, W. B. 1952. Gramophone studies of the stridulation of British grasshoppers. J. South West Essex Techn. Coll. 3(3): 170-180.

————————. 1963. Method in bio-acoustic terminology, p. 3 to 34. In R. G. Busnel [ed.]. Acoustic behaviour of animals. Elsevier Publishing Co., New York.

CHAVASSE, P., R. G. BUSNEL, F. PASQUINELLY and W. B. BROUGHTON. 1955. Propositions de définitions concernant l'acoustique appliquée aux insectes, p. 21 to 25. In R. G. Busnel [ed.]. L'acoustique des Orthoptères. Inst. Nat. Rech. Agron., Paris.

COMSTOCK, J. H. 1918. The wings of insects. Comstock Publishing Co., Ithaca, N. Y. 430 p.

DOLBEAR, A. E. 1897. The cricket as a thermometer. Amer. Nat. 31: 970-971.

DUMORTIER, B. 1963. The physical characteristics of sound emissions in Arthropoda, p. 346 to 373. In R. G. Busnel [ed.] Acoustic behaviour of animals. Elsevier Publishing Co., New York.

EDES, R. T. 1899. Relation of the chirping of the tree cricket (Oecanthus niveus) to temperature. Amer. Nat. 33: 935-938.

FRINGS, H. and M. FRINGS. 1957. The effect of temperature on chirp-rate of male cone-headed grasshopper, Neoconocephalus ensiger. J. Exp. Zool. 134: 411-425.

FULTON, B. B. 1925. Physiological variation in the snowy tree-cricket Oecanthus niveus deGeer. Ann. Ent. Soc. Amer. 18: 363-383.

———————. 1933. Inheritance of song in hybrids of two subspecies of N. fasciatus (Orthoptera). Ann. Ent. Soc. Amer. 26: 368-376.

———————. 1934. Rhythm, synchronism, and alternation in the stridulation of Orthoptera. J. Elisha Mitchell Sci. Soc. 50: 263-267.

HALLENBECK, C. 1949. Insect thermometers. Nat. Hist., N. Y. 58: 256-259, 285-287.

HASKELL,P. T. 1953. The stridulation behaviour of the domestic cricket. Brit. J. Anim. Behaviour 1: 120-121.

———————. 1961. Insect sounds. H. F. and G. Witherby Ltd., London. 189 p.

HINTON, H. E. 1948. Sound production in Lepidopterous pupae. Entomologist 81: 254-269.

HUBER, F. 1962. Central nervous control of sound production in crickets and some speculations on its evolution. Evolution 16: 429-442.

KREIDL, A. and J. REGEN. 1905. Physiologische Untersuchungen über Tierstimmen; stridulation von Gryllus campestris. Sitzber. Math. - Naturwiss. Kl. Akad. Wiss., Wien 114: 57-81.

LEROY, Y. 1962. Le signal sonore d'appel sexuel comme caractère spécifique chez les gryllides. Bull. Biol. 96: 755-774.

LUTZ, F. E. 1908. The variation and correlations of certain taxonomic characters of Gryllus. Carnegie Inst. Wash. Bull. 101. 63 p.

———————. 1938. The insect glee club at the microphone. Nat. Hist., N. Y. 42: 338-345, 378.

LUTZ, F. E. and W. R. HICKS. 1930. An analysis by movietone of a cricket's chirp (Gryllus assimilis). Amer. Mus. Novit. Bull. 420.14 p.

MYERS, J. G. 1929. Insect singers: a natural history of the cicadas. G. Routledge and S ons Ltd., London. 304 p.

PIERCE, G. W. 1948. The songs of insects. Harvard University Press, Cambridge, Massachusetts. 329 p.

PUMPHREY, R. J. and A. F. RAWDEN-SMITH. 1939. Frequency discrimination: a new theory. Nature, Lond. 143: 806.

RAKSHPAL, R. 1960. Sound producing organs and mechanisms of song production in field crickets of the genus Acheta Fabricius (Orthoptera, Gryllidae). Can. J. Zool. 38: 499-507.

REGEN, J. 1913. Ueber die Anlockung des Weibchens von Gryllus campestris L. durch telephonisch übertragende Stridulationslaute des Männchens. Ein Beitrag zur Frage der Orientierung bei den Insekten. Pflügers Arch. ges. Physiol. 155: 193-200.

SCHULL, A. F. 1907. The stridulation of the snowy tree cricket (Oecanthus niveus). Can. Ent. 39: 213-225.

TUXEN, S. L. 1967. Insektenstimmen. 1st rev. ed., Springer-Verlag, Heidelberg. 156 p.

WALKER, T. J. 1957. Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to the calling songs of the male. Ann. Ent. Soc. Amer. 50: 626-636.

————————. 1962. Factors responsible for intraspecific variation in the calling songs of crickets. Evolution 16: 407-428.

WOODS, E. F. 1959. Electronic prediction of swarming in bees. Nature, Lond. 184: 842-844.

# 6.0 APPENDIX

Table 1. Tegmina of G. veletis males: The percentage of the dorsal field occupied by each of its five subdivisions. (R and L refer to right and left tegmina respectively.)

| specimen | dorsal field area in $cm^2$ | basal area | harp | cordal area | mirror | apical area |
|---|---|---|---|---|---|---|
| 1 R | 0.432 | 19.76 | 23.32 | 18.94 | 10.22 | 20.68 |
| 1 L | 0.444 | 20.31 | 23.72 | 18.36 | 10.12 | 20.84 |
| 2 R | 0.517 | 20.98 | 22.15 | 18.28 | 10.49 | 21.36 |
| 2 L | 0.509 | 20.33 | 21.59 | 17.63 | 10.38 | 22.27 |
| 3 R | 0.461 | 21.64 | 23.52 | 18.43 | 11.18 | 17.15 |
| 3 L | 0.445 | 21.17 | 24.91 | 18.07 | 11.20 | 16.67 |
| 4 R | 0.373 | 22.77 | 22.69 | 19.10 | 12.42 | 15.12 |
| 4 L | 0.378 | 22.90 | 23.11 | 19.72 | 11.47 | 16.39 |
| 5 R | 0.280 | 20.25 | 26.50 | 20.77 | 13.18 | 11.15 |
| 5 L | 0.272 | 20.74 | 26.56 | 20.93 | 12.69 | 11.96 |
| 6 R | 0.441 | 21.16 | 24.29 | 15.92 | 11.20 | 18.08 |
| 7 R | 0.269 | 21.21 | 26.96 | 20.88 | 10.24 | 11.34 |
| 8 R | 0.278 | 22.16 | 26.76 | 21.74 | 11.86 | 11.26 |
| 9 R | 0.268 | 19.61 | 25.80 | 22.19 | 10.16 | 15.01 |
| 10 R | 0.280 | 21.65 | 25.54 | 20.99 | 12.18 | 12.86 |
| $\bar{x}$ | 0.377 | 21.11 | 24.50 | 19.46 | 11.27 | 16.14 |
| $\sigma$ | ± 0.094 | ± 0.99 | ± 1.78 | ± 1.75 | ± 1.01 | ± 3.92 |

Table 2. Tegmina of G. pennsylvanicus males: The percentage of the dorsal field occupied by each of its five subdivisions. (R and L refer to right and left tegmina respectively.)

| specimen | dorsal field area in $cm^2$ | basal area | harp | cordal area | mirror | apical area |
|---|---|---|---|---|---|---|
| 1 R | 0.337 | 21.48 | 26.82 | 21.04 | 11.56 | 10.71 |
| 1 L | 0.337 | 21.35 | 27.09 | 20.86 | 11.26 | 11.21 |
| 2 R | 0.345 | 21.42 | 25.36 | 20.71 | 11.62 | 11.75 |
| 2 L | 0.345 | 21.15 | 27.37 | 20.06 | 11.25 | 12.43 |
| 3 R | 0.383 | 20.97 | 21.74 | 17.53 | 11.23 | 19.74 |
| 3 L | 0.377 | 22.33 | 22.41 | 18.80 | 10.81 | 17.53 |
| 4 R | 0.327 | 20.17 | 24.47 | 22.15 | 11.50 | 13.01 |
| 4 L | 0.325 | 20.78 | 26.24 | 20.54 | 11.62 | 13.02 |
| 5 R | 0.327 | 21.40 | 25.79 | 21.51 | 11.35 | 12.34 |
| 5 L | 0.326 | 21.12 | 25.46 | 20.55 | 11.04 | 12.88 |
| 6 R | 0.370 | 20.69 | 24.52 | 22.15 | 12.01 | 13.32 |
| 7 R | 0.332 | 22.32 | 26.32 | 18.32 | 11.27 | 13.36 |
| 8 R | 0.424 | 30.47 | 25.30 | 18.61 | 9.71 | 13.43 |
| 9 R | 0.346 | 21.31 | 25.78 | 20.20 | 10.47 | 13.08 |
| 10 R | 0.323 | 21.14 | 29.37 | 19.40 | 11.68 | 13.18 |
| $\bar{x}$ | 0.348 | 21.87 | 25.60 | 20.16 | 11.23 | 13.40 |
| $\sigma$ | ±0.028 | ±2.44 | ±1.88 | ±1.38 | ±0.56 | ±2.31 |

Table 3. Tegmina of G. veletis and G. pennsylvanicus males: Areas of mirror, harp,and dorsal field. (R and L refer to right and left tegmina respectively.)

| | G. veletis | | | G. pennsylvanicus | | |
|---|---|---|---|---|---|---|
| specimen | mirror area in $cm^2$ | harp area in $cm^2$ | dorsal field area in $cm^2$ | mirror area in $cm^2$ | harp area in $cm^2$ | dorsal field area in $cm^2$ |
| 1 R | 0.044 | 0.101 | 0.432 | 0.039 | 0.090 | 0.337 |
| 1 L | 0.045 | 0.105 | 0.444 | 0.038 | 0.091 | 0.337 |
| 2 R | 0.054 | 0.115 | 0.517 | 0.040 | 0.088 | 0.345 |
| 2 L | 0.053 | 0.110 | 0.509 | 0.039 | 0.094 | 0.345 |
| 3 R | 0.052 | 0.108 | 0.461 | 0.043 | 0.083 | 0.383 |
| 3 L | 0.050 | 0.111 | 0.445 | 0.041 | 0.085 | 0.377 |
| 4 R | 0.046 | 0.085 | 0.373 | 0.038 | 0.080 | 0.327 |
| 4 L | 0.043 | 0.087 | 0.378 | 0.038 | 0.085 | 0.325 |
| 5 R | 0.037 | 0.074 | 0.280 | 0.037 | 0.084 | 0.327 |
| 5 L | 0.035 | 0.072 | 0.272 | 0.036 | 0.083 | 0.326 |
| 6 R | 0.049 | 0.107 | 0.441 | 0.044 | 0.091 | 0.370 |
| 7 R | 0.028 | 0.073 | 0.269 | 0.037 | 0.087 | 0.332 |
| 8 R | 0.033 | 0.074 | 0.278 | 0.041 | 0.107 | 0.424 |
| 9 R | 0.027 | 0.069 | 0.268 | 0.036 | 0.089 | 0.346 |
| 10 R | 0.034 | 0.069 | 0.280 | 0.038 | 0.095 | 0.323 |
| $\bar{x}$ | 0.042 | 0.091 | 0.377 | 0.039 | 0.089 | 0.348 |
| $\sigma$ | ± 0.009 | ± 0.018 | ± 0.094 | ± 0.002 | ± 0.007 | ± 0.028 |

Table 4. Tegmina of G. veletis and G. pennsylvanicus males: The relationship between number of file teeth, file length, and dorsal field area. (R and L refer to right and left tegmina respectively.)

| | G. veletis | | | G. pennsylvanicus | | |
|---|---|---|---|---|---|---|
| specimen | number of file teeth | file length in cm | dorsal field area in $cm^2$ | number of file teeth | file length in cm | dorsal field area in $cm^2$ |
| 1 R | 150 | 0.331 | 0.432 | 158 | 0.333 | 0.337 |
| 1 L | 151 | 0.330 | 0.444 | 154 | 0.316 | 0.337 |
| 2 R | 155 | 0.361 | 0.517 | 156 | 0.344 | 0.345 |
| 2 L | 154 | 0.351 | 0.509 | 152 | 0.329 | 0.345 |
| 3 R | 154 | 0.351 | 0.461 | 150 | 0.317 | 0.383 |
| 3 L | 147 | 0.326 | 0.445 | 148 | 0.319 | 0.377 |
| 4 R | 144 | 0.300 | 0.373 | 156 | 0.318 | 0.327 |
| 4 L | 138 | 0.296 | 0.378 | 152 | 0.311 | 0.325 |
| 5 R | 149 | 0.296 | 0.280 | 152 | 0.324 | 0.327 |
| 5 L | 142 | 0.286 | 0.272 | 141 | 0.301 | 0.326 |
| 6 R | 139 | 0.338 | 0.441 | 159 | 0.357 | 0.370 |
| 7 R | 143 | 0.296 | 0.269 | 156 | 0.335 | 0.332 |
| 8 R | 146 | 0.291 | 0.278 | 150 | 0.367 | 0.424 |
| 9 R | 151 | 0.266 | 0.268 | 161 | 0.322 | 0.346 |
| 10 R | 149 | 0.315 | 0.280 | 163 | 0.320 | 0.323 |
| $\bar{x}$ | 147.5 | 0.316 | 0.377 | 153.9 | 0.328 | 0.348 |
| $\sigma$ | ± 5.3 | ±0.029 | ±0.094 | ± 5.6 | ±0.020 | ±0.028 |

Table 5. G. veletis males: A comparison between the right and left tegmina.

(R and L refer to right and left tegmina respectively.)

| specimen | dorsal field area in $cm^2$ | | mirror area in $cm^2$ | | harp area in $cm^2$ | | file length in cm | | number of file teeth | |
|---|---|---|---|---|---|---|---|---|---|---|
| | R | L | R | L | R | L | R | L | R | L |
| 1 | 0.432 | 0.444 | 0.044 | 0.045 | 0.101 | 0.105 | 0.331 | 0.330 | 150 | 151 |
| 2 | 0.517 | 0.509 | 0.054 | 0.053 | 0.115 | 0.110 | 0.361 | 0.351 | 155 | 154 |
| 3 | 0.461 | 0.445 | 0.052 | 0.050 | 0.108 | 0.111 | 0.351 | 0.326 | 154 | 147 |
| 4 | 0.373 | 0.378 | 0.046 | 0.043 | 0.085 | 0.087 | 0.300 | 0.296 | 144 | 138 |
| 5 | 0.280 | 0.272 | 0.037 | 0.035 | 0.074 | 0.072 | 0.296 | 0.286 | 149 | 142 |
| $\bar{x}$ | 0.413 | 0.410 | 0.047 | 0.045 | 0.097 | 0.097 | 0.328 | 0.318 | 150.4 | 146.4 |
| $\sigma$ | ±0.091 | ±0.090 | ±0.007 | ±0.007 | ±0.017 | ±0.017 | ±0.031 | ±0.028 | ±4.4 | ±6.5 |

Table 6. G. pennsylvanicus males: A comparison between the right and left tegmina. (R and L refer to right and left tegmina respectively.)

| specimen | dorsal field area in $cm^2$ | | mirror area in $cm^2$ | | harp area in $cm^2$ | | file length in cm | | number of file teeth | |
|---|---|---|---|---|---|---|---|---|---|---|
| | R | L | R | L | R | L | R | L | R | L |
| 1 | 0.337 | 0.337 | 0.039 | 0.038 | 0.090 | 0.091 | 0.333 | 0.316 | 158 | 154 |
| 2 | 0.345 | 0.345 | 0.040 | 0.039 | 0.088 | 0.094 | 0.344 | 0.329 | 156 | 152 |
| 3 | 0.383 | 0.377 | 0.043 | 0.041 | 0.083 | 0.085 | 0.317 | 0.319 | 150 | 148 |
| 4 | 0.327 | 0.325 | 0.038 | 0.038 | 0.080 | 0.085 | 0.318 | 0.311 | 156 | 152 |
| 5 | 0.327 | 0.326 | 0.037 | 0.036 | 0.084 | 0.083 | 0.324 | 0.301 | 152 | 141 |
| $\bar{x}$ | 0.344 | 0.342 | 0.039 | 0.038 | 0.085 | 0.088 | 0.327 | 0.315 | 154.4 | 149.4 |
| $\sigma \pm$ | 0.024 | ±0.022 | ±0.003 | ±0.002 | ±0.001 | ±0.003 | ±0.014 | ±0.017 | ±3.3 | ±5.2 |

Table 7. Tegmina of G. veletis males: The percentage of the total number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end. (R and L refer to right and left tegmina respectively.)

| specimen | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 R | 18.67 | 10.67 | 10.00 | 8.67 | 8.67 | 8.00 | 8.67 | 8.67 | 9.33 | 8.67 |
| 1 L | 19.87 | 11.26 | 9.93 | 8.61 | 8.61 | 7.29 | 7.95 | 8.61 | 8.61 | 9.27 |
| 2 R | 20.65 | 11.61 | 9.68 | 7.74 | 8.39 | 7.74 | 7.74 | 8.39 | 9.03 | 9.03 |
| 2 L | 18.83 | 11.04 | 9.74 | 9.09 | 8.44 | 7.79 | 8.44 | 7.79 | 9.09 | 9.74 |
| 3 R | 20.13 | 12.34 | 9.09 | 9.09 | 8.44 | 7.14 | 8.44 | 7.79 | 9.09 | 8.44 |
| 3 L | 19.05 | 11.57 | 10.20 | 9.52 | 8.16 | 8.16 | 7.48 | 8.16 | 8.84 | 8.84 |
| 4 R | 19.44 | 11.11 | 9.72 | 9.03 | 8.33 | 8.33 | 7.64 | 8.33 | 8.33 | 9.72 |
| 4 L | 18.12 | 11.59 | 10.15 | 8.70 | 8.70 | 7.97 | 7.97 | 8.70 | 9.42 | 8.70 |
| 5 R | 17.45 | 12.08 | 10.74 | 10.07 | 8.73 | 8.05 | 8.05 | 8.73 | 8.05 | 8.05 |
| 5 L | 18.31 | 12.68 | 11.27 | 9.16 | 9.16 | 7.75 | 7.75 | 8.45 | 8.45 | 7.04 |
| 6 R | 21.58 | 11.51 | 9.35 | 8.63 | 8.63 | 7.91 | 7.19 | 7.91 | 8.63 | 8.63 |
| 7 R | 17.48 | 11.89 | 9.09 | 9.09 | 8.39 | 8.39 | 8.39 | 8.39 | 9.09 | 9.79 |
| 8 R | 18.49 | 11.64 | 10.27 | 9.59 | 8.90 | 8.90 | 7.53 | 8.90 | 8.22 | 7.53 |
| 9 R | 16.56 | 11.92 | 9.93 | 9.27 | 8.61 | 8.61 | 8.61 | 7.95 | 8.61 | 9.93 |
| 10 R | 18.12 | 12.75 | 10.74 | 8.73 | 8.73 | 8.05 | 8.73 | 8.05 | 8.05 | 8.05 |
| $\bar{x}$ | 18.85 | 11.71 | 9.99 | 9.00 | 8.59 | 8.01 | 8.04 | 8.32 | 8.72 | 8.76 |
| $\sigma$ | ±1.32 | ±0.59 | ±0.48 | ±0.54 | ±0.24 | ±0.46 | ±0.48 | ±0.36 | ±0.46 | ±0.85 |

Table 8. Tegmina of G. pennsylvanicus males: The percentage of the total number of teeth found on each consecutive 10% of the length of the file, from the medial to the lateral end. (R and L refer to right and left tegmina respectively.)

| specimen | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 R | 17.09 | 12.66 | 10.13 | 8.86 | 9.49 | 8.23 | 8.23 | 8.23 | 8.86 | 8.23 |
| 1 L | 17.53 | 12.34 | 10.39 | 9.09 | 8.44 | 8.44 | 8.44 | 8.44 | 8.44 | 8.44 |
| 2 R | 17.95 | 11.54 | 10.26 | 9.62 | 8.33 | 8.33 | 8.33 | 8.33 | 8.97 | 8.33 |
| 2 L | 19.08 | 11.84 | 9.87 | 9.87 | 8.55 | 8.55 | 7.90 | 7.90 | 8.55 | 7.90 |
| 3 R | 16.67 | 12.67 | 10.67 | 9.33 | 8.67 | 8.67 | 8.00 | 8.67 | 8.67 | 8.00 |
| 3 L | 17.57 | 12.16 | 10.14 | 10.14 | 8.78 | 8.78 | 8.11 | 8.11 | 7.43 | 8.78 |
| 4 R | 16.67 | 12.82 | 10.90 | 9.62 | 9.62 | 8.33 | 8.33 | 7.69 | 8.33 | 7.69 |
| 4 L | 17.11 | 12.50 | 10.53 | 10.53 | 8.55 | 7.90 | 7.90 | 8.55 | 8.55 | 7.90 |
| 5 R | 19.08 | 11.84 | 10.53 | 9.87 | 9.21 | 7.90 | 8.55 | 7.90 | 7.24 | 7.90 |
| 5 L | 17.02 | 11.35 | 10.64 | 9.22 | 8.51 | 8.51 | 7.80 | 9.22 | 8.51 | 9.22 |
| 6 R | 19.50 | 11.95 | 10.69 | 9.43 | 8.18 | 8.18 | 8.18 | 8.18 | 8.18 | 7.55 |
| 7 R | 18.59 | 12.18 | 10.26 | 8.97 | 8.97 | 8.33 | 8.33 | 8.33 | 8.97 | 7.05 |
| 8 R | 19.33 | 12.00 | 10.67 | 9.33 | 8.67 | 8.00 | 8.67 | 8.00 | 8.00 | 8.00 |
| 9 R | 16.77 | 12.42 | 9.94 | 9.32 | 9.32 | 8.08 | 8.70 | 8.08 | 8.70 | 8.70 |
| 10 R | 17.79 | 12.27 | 9.82 | 9.20 | 8.59 | 8.59 | 7.98 | 8.59 | 9.20 | 7.98 |
| $\bar{x}$ | 17.85 | 12.17 | 10.36 | 9.49 | 8.79 | 8.32 | 8.23 | 8.28 | 8.44 | 8.11 |
| $\sigma$ | ±1.01 | ±0.42 | ±0.33 | ±0.45 | ±0.43 | ±0.27 | ±0.28 | ±0.38 | ±0.55 | ±0.53 |

Table 9. G. veletis and G. pennsylvanicus calling songs: Percentage of chirps with three, four, five,and six pulses.

| species | number of chirps analyzed | 3 pulses | 4 pulses | 5 pulses | 6 pulses |
|---|---|---|---|---|---|
| G. veletis | 75 | 22.7 | 53.3 | 20.0 | 4.0 |
| G. pennsylvanicus | 45 | 73.3 | 26.7 | 0.0 | 0.0 |

Table 10. G. veletis and G. pennsylvanicus calling songs: Percentage of sonagram chirps beginning with faint, short marks.

| species | number of chirps analyzed | 3 pulses | 4 pulses | 5 pulses | 6 pulses |
|---|---|---|---|---|---|
| G. veletis | 75 | 0.0 | 35.0 | 46.7 | 33.3 |
| G. pennsylvanicus | 45 | 8.3 | 0.0 | 0.0 | 0.0 |

Table 11. G. veletis calling song: The relationship between temperature, pulse duration, and pulse interval.

| temperature °C | specimen | grand average duration of each pulse in msecs 1 | 2 | 3 | 4 | 5 | 6 | $\bar{x}$ | grand average duration of each pulse interval in msecs 1-2 | 2-3 | 3-4 | 4-5 | 5-6 | $\bar{x}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15.2 | 1 | 20.4 | 22.3 | 23.9 | 20.4 | | | 21.75 | 42.0 | 47.0 | 47.4 | | | 45.47 |
| 20.0 | 1 | 14.6 | 16.6 | 18.1 | 18.9 | | | 17.05 | 30.4 | 31.6 | 34.7 | | | 32.23 |
| 25.7 | 1 | 15.4 | 18.9 | 19.6 | 20.8 | | | 18.68 | 18.1 | 21.6 | 27.3 | | | 22.33 |
| 16.6 | 2 | 9.2 | 15.8 | 21.2 | 20.0 | 20.0 | | 17.24 | 23.9 | 24.3 | 31.6 | 34.7 | | 28.63 |
| 24.6 | 2 | 8.1 | 12.7 | 12.3 | 14.2 | | | 11.83 | 20.8 | 24.3 | 26.6 | | | 23.90 |
| 26.2 | 2 | 6.2 | 11.6 | 13.5 | 13.1 | 13.5 | | 11.58 | 19.6 | 21.9 | 25.4 | 32.0 | | 24.73 |
| 29.7 | 2 | 10.4 | 13.5 | 17.3 | 17.7 | 18.9 | | 15.56 | 9.6 | 13.5 | 16.6 | 17.7 | | 14.35 |
| 31.0 | 2 | 4.6 | 10.0 | 12.7 | 12.3 | | | 9.90 | 17.7 | 20.4 | 22.9 | | | 20.33 |
| 21.9 | 3 | 10.8 | 21.6 | 20.0 | 19.3 | | | 17.93 | 16.6 | 22.7 | 26.6 | | | 21.97 |
| 32.8 | 3 | 13.5 | 16.2 | 15.0 | 15.4 | 16.2 | | 15.26 | 10.8 | 13.1 | 17.7 | 24.3 | | 16.48 |
| 29.5 | 4 | 7.7 | 13.9 | 15.4 | 16.6 | 14.6 | | 13.64 | 16.2 | 15.8 | 19.3 | 18.9 | | 17.55 |
| 19.4 | 5 | 12.3 | 16.2 | 16.9 | 17.1 | 14.2 | 16.2 | 15.48 | 20.4 | 27.3 | 29.6 | 34.7 | 40.0 | 30.40 |
| 32.0 | 5 | 13.5 | 13.9 | 13.1 | 12.3 | | | 13.20 | 10.8 | 16.2 | 19.6 | | | 15.53 |
| 16.6 | 6 | 13.5 | 21.6 | 22.7 | 21.2 | 23.9 | | 20.58 | 28.9 | 28.1 | 33.5 | 34.7 | | 31.30 |
| 29.6 | 8 | 9.6 | 18.5 | 18.9 | 16.2 | 18.5 | 20.0 | 16.95 | 11.2 | 11.2 | 14.2 | 25.4 | 18.5 | 16.10 |
| 29.6 | 9 | 11.2 | 15.0 | 17.7 | 21.2 | 26.6 | | 18.34 | 22.3 | 16.2 | 13.1 | 12.7 | | 16.08 |
| 16.8 | 10 | 16.6 | 21.6 | 21.6 | | | | 19.93 | 35.8 | 39.3 | | | | 37.55 |
| 19.2 | 10 | 17.7 | 18.1 | 17.7 | 19.3 | | | 18.20 | 31.2 | 33.9 | 37.7 | | | 34.27 |
| 24.0 | 10 | 11.6 | 14.6 | 16.9 | 15.4 | | | 14.63 | 30.0 | 29.3 | 41.6 | | | 33.63 |
| 25.2 | 10 | 7.3 | 16.2 | 18.1 | 15.8 | | | 14.35 | 20.8 | 23.5 | 26.2 | | | 23.50 |
| 25.8 | 10 | 16.2 | 20.0 | 17.3 | | | | 17.83 | 25.0 | 27.7 | | | | 26.35 |
| 26.2 | 10 | 8.1 | 16.2 | 17.7 | | | | 14.00 | 25.4 | 28.9 | | | | 27.15 |
| 26.4 | 10 | 16.4 | 19.9 | 20.0 | 20.4 | | | 19.18 | 17.6 | 18.7 | 24.3 | | | 20.20 |
| 29.2 | 10 | 11.2 | 17.7 | 16.2 | 16.2 | | | 15.33 | 17.7 | 19.6 | 25.0 | | | 20.77 |
| 31.6 | 10 | 10.4 | 17.7 | 13.9 | | | | 14.00 | 17.3 | 20.4 | | | | 18.85 |
| $\bar{x}$ 24.9 | | 11.86 | 16.81 | 17.51 | | | | 16.10 | 21.60 | 23.86 | | | | 24.79 |

Table 12. G. pennsylvanicus calling song: The relationship between temperature, pulse duration, and pulse interval.

| temperature °C | specimen | grand average duration of each pulse in msecs 1 | 2 | 3 | 4 | $\bar{x}$ | grand average duration of each pulse interval in msecs 1-2 | 2-3 | 3-4 | $\bar{x}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 24.3 | 27 | 14.2 | 21.9 | 21.8 | 22.6 | 20.13 | 26.4 | 25.0 | 26.4 | 25.93 |
| 27.7 | 27 | 16.2 | 20.0 | 20.8 | | 19.00 | 25.8 | 24.5 | | 25.15 |
| 28.0 | 27 | 11.4 | 14.2 | 18.5 | 19.3 | 15.85 | 28.2 | 28.2 | 30.0 | 28.80 |
| 26.4 | 4 | 19.1 | 19.3 | 18.5 | | 18.97 | 19.5 | 27.2 | | 23.35 |
| 28.0 | 4 | 12.6 | 19.3 | 20.6 | | 17.50 | 24.4 | 25.9 | | 25.15 |
| 25.4 | 33 | 15.0 | 14.6 | 15.4 | | 15.00 | 26.2 | 40.4 | | 33.30 |
| 27.6 | 33 | 13.9 | 14.2 | 16.9 | | 15.00 | 25.4 | 33.9 | | 29.65 |
| 27.2 | 2 | 6.9 | 16.2 | 20.0 | | 14.37 | 29.5 | 26.2 | | 27.85 |
| 28.0 | 2 | 16.2 | 21.0 | 23.9 | 23.9 | 21.25 | 23.3 | 24.1 | 30.0 | 25.80 |
| 24.6 | 10 | 11.9 | 16.8 | 19.1 | | 15.93 | 36.6 | 35.0 | | 35.80 |
| 28.6 | 23 | 14.1 | 19.5 | 16.7 | | 16.77 | 23.6 | 25.9 | | 24.75 |
| 23.6 | 5 | 12.9 | 17.7 | 23.3 | 18.7 | 17.90 | 19.5 | 22.9 | 29.8 | 24.07 |
| 26.4 | 1 | 13.1 | 15.4 | 15.8 | | 14.77 | 21.9 | 32.3 | | 27.10 |
| 26.7 | 11 | 15.2 | 16.8 | 16.4 | | 16.13 | 25.8 | 25.0 | | 25.40 |
| 22.6 | 18 | 16.9 | 18.7 | 20.3 | 17.7 | 18.40 | 18.2 | 30.0 | 32.0 | 26.73 |
| $\bar{x}$ 26.3 | | 13.97 | 17.71 | 19.20 | | 17.13 | 24.95 | 28.43 | | 27.26 |

Table 13. G. veletis calling song: The relationship between temperature and dominant frequency.

| temperature °C | specimen | grand average dominant frequency of each pulse in kcps 1 | 2 | 3 | 4 | 5 | 6 | $\bar{x}$ | mean frequency range in kcps |
|---|---|---|---|---|---|---|---|---|---|
| 15.2 | 1 | 4.05 | 4.03 | 4.03 | 4.09 | | | 4.05 | 2.71 - 5.34 |
| 20.0 | 1 | 3.94 | 3.98 | 4.03 | 4.03 | | | 3.99 | 2.71 - 5.21 |
| 25.7 | 1 | 4.64 | 4.73 | 4.71 | 4.68 | | | 4.69 | 3.24 - 6.00 |
| 16.6 | 2 | 3.86 | 3.99 | 4.06 | 4.09 | 4.09 | | 4.02 | 2.45 - 5.61 |
| 24.6 | 2 | 4.20 | 4.33 | 4.29 | 4.33 | | | 4.29 | 3.24 - 5.34 |
| 26.2 | 2 | 4.14 | 4.25 | 4.27 | 4.31 | 4.36 | | 4.26 | 2.84 - 5.74 |
| 29.7 | 2 | 4.14 | 4.31 | 4.77 | 4.52 | 5.21 | | 4.59 | 2.71 - 6.00 |
| 31.0 | 2 | 4.07 | 4.27 | 4.46 | 4.53 | | | 4.33 | 3.24 - 5.61 |
| 21.9 | 3 | 4.90 | 5.08 | 5.06 | 5.01 | | | 5.01 | 3.63 - 6.66 |
| 32.8 | 3 | 5.21 | 5.39 | 5.41 | 5.49 | 5.34 | | 5.37 | 3.89 - 6.79 |
| 19.4 | 5 | 4.18 | 4.33 | 4.40 | 4.31 | 4.33 | 4.42 | 4.33 | 2.84 - 5.87 |
| 32.0 | 5 | 5.33 | 5.29 | 5.35 | 5.31 | | | 5.32 | 3.37 - 6.79 |
| 29.6 | 8 | 4.60 | 4.75 | 4.77 | 4.73 | 4.79 | 4.75 | 4.73 | 3.37 - 6.00 |
| 29.6 | 9 | 3.85 | 4.11 | 4.20 | 4.20 | 4.26 | | 4.13 | 2.71 - 5.74 |
| 16.8 | 10 | 4.18 | 4.25 | 4.25 | | | | 4.22 | 3.10 - 5.34 |
| 19.2 | 10 | 3.98 | 4.07 | 4.05 | 4.05 | | | 4.04 | 2.84 - 5.21 |
| 24.0 | 10 | 4.31 | 4.31 | 4.36 | 4.38 | | | 4.34 | 3.10 - 5.74 |
| 25.2 | 10 | 4.29 | 4.42 | 4.44 | 4.42 | | | 4.39 | 3.10 - 5.87 |
| 25.8 | 10 | 4.31 | 4.49 | 4.38 | | | | 4.39 | 2.97 - 5.74 |
| 26.2 | 10 | 4.31 | 4.49 | 4.53 | | | | 4.44 | 3.10 - 5.87 |
| 26.4 | 10 | 4.51 | 4.53 | 4.53 | 4.55 | | | 4.53 | 3.10 - 5.87 |
| 29.2 | 10 | 4.27 | 4.42 | 4.38 | 4.42 | | | 4.37 | 3.10 - 5.74 |
| 31.6 | 10 | 4.49 | 4.60 | 4.42 | | | | 4.50 | 2.97 - 6.00 |
| $\bar{x}$ 25.2 | | 4.34 | 4.45 | 4.49 | | | | 4.45 | 3.06 - 5.83 |

Table 14. G. pennsylvanicus calling song: The relationship between temperature and dominant frequency.

| temperature °C | specimen | grand average frequency of each pulse in kcps 1 | 2 | 3 | 4 | $\bar{x}$ | mean frequency range in kcps |
|---|---|---|---|---|---|---|---|
| 24.3 | 27 | 4.09 | 4.11 | 4.14 | 4.14 | 4.12 | 2.84 - 5.47 |
| 27.7 | 27 | 4.18 | 4.18 | 4.22 | | 4.19 | 2.97 - 5.47 |
| 28.0 | 27 | 4.20 | 4.27 | 4.31 | 4.29 | 4.27 | 3.10 - 5.47 |
| 26.4 | 4 | 4.09 | 4.36 | 4.44 | | 4.30 | 2.84 - 5.87 |
| 28.0 | 4 | 3.96 | 4.09 | 4.16 | | 4.07 | 2.58 - 5.61 |
| 25.4 | 33 | 4.16 | 4.29 | 4.20 | | 4.22 | 2.84 - 5.47 |
| 27.6 | 33 | 4.25 | 4.33 | 4.29 | | 4.29 | 2.97 - 5.47 |
| 27.2 | 2 | 3.61 | 3.65 | 3.65 | | 3.64 | 2.45 - 4.82 |
| 28.0 | 2 | 3.61 | 3.65 | 3.61 | 3.63 | 3.63 | 2.45 - 4.82 |
| 24.6 | 10 | 4.42 | 4.53 | 4.49 | | 4.48 | 3.24 - 5.87 |
| 28.6 | 23 | 4.44 | 4.40 | 4.38 | | 4.41 | 2.84 - 6.00 |
| 23.6 | 5 | 3.85 | 4.14 | 4.09 | 4.09 | 4.04 | 2.84 - 5.47 |
| 26.4 | 1 | 3.65 | 3.76 | 3.74 | | 3.72 | 2.58 - 4.95 |
| 26.7 | 11 | 4.55 | 4.53 | 4.55 | | 4.54 | 3.24 - 5.74 |
| 22.6 | 18 | 3.70 | 3.87 | 3.87 | 3.88 | 3.83 | 2.45 - 5.34 |
| 26.3 | $\bar{x}$ | 4.05 | 4.14 | 4.14 | | 4.13 | 2.82 - 5.46 |

Table 15. G. veletis calling song: The relationship between temperature and grand average pulse rate.

| specimen | temperature °C | pulse rate in pulses/sec |
|---|---|---|
| 1 | 15.2 | 14.9 |
| 1 | 20.0 | 20.7 |
| 1 | 25.7 | 26.0 |
| 2 | 16.6 | 21.6 |
| 2 | 24.6 | 27.7 |
| 2 | 26.2 | 30.5 |
| 2 | 29.7 | 36.9 |
| 2 | 31.0 | 34.3 |
| 3 | 21.9 | 26.0 |
| 3 | 32.8 | 34.2 |
| 4 | 29.5 | 31.2 |
| 5 | 19.4 | 22.7 |
| 5 | 32.0 | 35.6 |
| 6 | 16.6 | 20.0 |
| 8 | 29.6 | 31.6 |
| 9 | 29.6 | 31.4 |
| 10 | 16.8 | 17.7 |
| 10 | 19.2 | 19.5 |
| 10 | 24.0 | 20.9 |
| 10 | 25.2 | 27.0 |
| 10 | 25.8 | 22.8 |
| 10 | 26.2 | 25.6 |
| 10 | 26.4 | 27.2 |
| 10 | 29.2 | 29.4 |
| 10 | 31.6 | 31.0 |
| $\bar{x}$ | 24.9 | 26.7 |

Table 16. G. pennsylvanicus calling song: The relationship between temperature and grand average pulse rate.

| specimen | temperature °C | pulse rate in pulses/sec |
|---|---|---|
| 27 | 24.3 | 21.9 |
| 27 | 27.7 | 23.1 |
| 27 | 28.0 | 23.0 |
| 4 | 26.4 | 24.3 |
| 4 | 28.0 | 24.5 |
| 33 | 25.4 | 21.5 |
| 33 | 27.6 | 23.1 |
| 2 | 27.2 | 25.2 |
| 2 | 28.0 | 23.4 |
| 10 | 24.6 | 20.1 |
| 23 | 28.6 | 24.1 |
| 5 | 23.6 | 24.3 |
| 1 | 26.4 | 24.4 |
| 11 | 26.7 | 24.2 |
| 18 | 22.6 | 22.5 |
| $\bar{x}$ | 26.3 | 23.3 |

Table 17. G. veletis calling song: The relationship between temperature and number of teeth struck per pulse.

| temperature °C | | specimen | number of teeth struck during the grand average duration of each pulse 1 | 2 | 3 | 4 | 5 | 6 | $\bar{x}$ | % of teeth struck |
|---|---|---|---|---|---|---|---|---|---|---|
| 15.2 | | 1 | 82.62 | 89.87 | 96.32 | 83.44 | | | 88.06 | 59.70 |
| 20.0 | | 1 | 57.52 | 66.07 | 72.94 | 76.17 | | | 68.18 | 46.22 |
| 25.7 | | 1 | 71.46 | 89.40 | 92.32 | 97.34 | | | 87.63 | 59.41 |
| 16.6 | | 2 | 35.51 | 63.04 | 86.07 | 81.80 | 81.80 | | 69.64 | 47.21 |
| 24.6 | | 2 | 34.02 | 54.99 | 52.77 | 61.49 | | | 50.82 | 34.39 |
| 26.2 | | 2 | 25.67 | 49.30 | 57.65 | 56.46 | 58.86 | | 49.59 | 33.62 |
| 29.7 | | 2 | 43.06 | 58.19 | 82.52 | 80.00 | 98.47 | | 72.45 | 49.12 |
| 31.0 | | 2 | 18.72 | 42.70 | 56.64 | 55.72 | | | 43.45 | 29.46 |
| 21.9 | | 3 | 52.92 | 109.73 | 101.20 | 96.69 | | | 90.14 | 61.11 |
| 32.8 | | 3 | 70.34 | 87.32 | 81.15 | 84.55 | 86.51 | | 81.97 | 55.57 |
| 19.4 | | 5 | 51.41 | 70.15 | 74.36 | 73.70 | 61.49 | 71.60 | 67.12 | 45.51 |
| 32.0 | | 5 | 71.96 | 73.53 | 70.09 | 65.31 | | | 70.22 | 47.61 |
| 29.6 | | 8 | 44.16 | 87.88 | 90.15 | 76.63 | 88.62 | 95.00 | 80.41 | 54.52 |
| 29.6 | | 9 | 43.12 | 61.65 | 74.34 | 89.04 | 111.32 | | 75.89 | 51.45 |
| 16.8 | | 10 | 69.39 | 91.80 | 91.80 | | | | 84.33 | 57.17 |
| 19.2 | | 10 | 70.45 | 73.67 | 71.69 | 78.17 | | | 73.50 | 49.83 |
| 24.0 | | 10 | 50.00 | 62.93 | 73.68 | 67.45 | | | 63.52 | 43.06 |
| 25.2 | | 10 | 31.32 | 71.60 | 80.36 | 69.84 | | | 63.28 | 42.90 |
| 25.8 | | 10 | 69.82 | 69.80 | 75.77 | | | | 78.46 | 53.19 |
| 26.2 | | 10 | 34.91 | 72.74 | 80.18 | | | | 62.61 | 42.45 |
| 26.4 | | 10 | 73.96 | 90.15 | 91.51 | 92.82 | | | 87.11 | 50.91 |
| 29.2 | | 10 | 47.82 | 78.23 | 70.96 | 71.60 | | | 67.15 | 45.53 |
| 31.6 | | 10 | 46.70 | 81.42 | 61.44 | | | | 63.19 | 42.84 |
| 25.2 | $\bar{x}$ | | 52.04 | 74.62 | 77.65 | | | | 71.25 | 48.31 |